UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

SPRUCING UP EASTERN CANADIAN MIXEDWOODS:

DOES WHITE SPRUCE (*PICEA GLAUCA*) RESPOND TO PARTIAL HARVESTING?

DISSERTATION

PRESENTED

AS PARTIAL REQUIREMENT

OF THE MASTERS OF BIOLOGY

EXTENDED FROM

L'UNIVERSITÉ DU QUÉBEC À MONTRÉAL

BY

JESSICA SMITH

FEBRUARY 2015

UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

RÉPONSES EN CROISSANCE RADIALE ET VOLUMÉTRIQUE DE L'ÉPINETTE BLANCHE (*PICEA GLAUCA*) SUITE AUX COUPES PARTIELLES DANS DES PEUPLEMENTS MIXTES

MÉMOIRE

PRÉSENTÉ

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN BIOLOGIE

EXTENSIONNÉE

DE

L'UNIVERSITÉ DU QUÉBEC À MONTRÉAL

PAR

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FÉVRIER 2015

ACKNOWLEDGEMENTS

Special thanks to my supervisor Dr. Brian Harvey and co-supervisor Dr. Ahmed Koubaa, for their expertise, insights and guidance throughout the duration of my graduate studies at the University of Quebec in Abitibi-Témiscamingue (UQAT). Sincere gratitude to Brian for taking me on as a student despite my limited experience in boreal forestry ecology. Thank you for believing in me and encouraging me to embrace the French language and cultures of northwestern Quebec. Thank you for the memorable experience and opportunity to present my project at the IUFRO International Conference on Uneven-aged Silviculture in Zurich, Switzerland.

Thank you to Jean-Marc St. Armant (formerly of Tembec Industries) and Yvon Grenier (formerly of UQAT) for their dedicated work in initiating the project and establishing the partial harvesting experiment. Thank you to my committee members Dr. Francine Tremblay of UQAT and Dr. Alexis Achim of Laval University, for reviewing my thesis. I am grateful for the support of numerous colleagues including Dr. Suzanne Brais, Dr. Marc Mazerolle, Dr. Igor Drobyshev and Dr. Alain Leduc for their support in many aspects of my master's project. I am indebted to Dr. Arun Bose for paving the way and providing valuable guidance and assistance in many facets of my thesis. I would like to acknowledge the field technicians: Suzie Rollin, Elizabeth Turcotte and Alfred Coulombe as well as the graduate students who helped with field measurements, data collection and sample preparation.

This project was financially supported through the NSERC Collaborative Research and Development Grant CRDPJ 395368-09 (Eastern boreal mixedwoods: Multiscale analysis of stand structure, dynamics and silviculture) awarded to Dr. Brian Harvey. I would also like to acknowledge the Mitacs Accelerate program and the UQAM-UQAT Industrial Chair in Sustainable Forest Development who provided additional funding for the project. Thanks to Tembec Industries for acting as industrial partner, specifically warm thanks to Geneviève Labrecque and Louis Dumas for showing an interest in the project.

Special thanks to my parents David and Ellen Smith, for providing much needed moral support and long lasting encouragement. Thanks to the many friends at UQAT who helped this Ontario girl adapt to university life in Quebec and for making it so easy to fit in.

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RÉSUMÉ

Les peuplements mixtes de la région de l'Abitibi-Témiscamingue sont souvent caractérisés par une dominance d'espèces intolérantes à l'ombre, comme le peuplier faux-tremble (*Populus tremuloides* Michx.), avec une forte composante de conifères plus tolérants, comme le sapin baumier (*Abies balsamea* (L.) Mill.) et l'épinette blanche (*Picea glauca* (Moench.) Voss) situés davantage dans les strates inférieures de la canopée. Les espèces feuillues intolérantes et résineuses tolérantes sont généralement récoltées en même temps en utilisant les CPRS (coupes avec protection de la régénération et des sols), la principale méthode de récolte utilisée au Québec. En raison des différences en termes de dynamiques de croissance entre le peuplier faux-tremble et les arbres résineux, les conifères se situent encore principalement dans la strate de gaules ou des petites classes commerciales quand le peuplier a atteint sa croissance maximale et est arrivé au stade de récolte. Cela a développé un intérêt pour la diversification des traitements sylvicoles mieux adaptés à la structure et la dynamique des peuplements mixtes. Dans certaines conditions, les coupes partielles ont été promues comme une méthode alternative aux CPRS et comme un outil à l'échelle du peuplement, à appliquer dans le contexte de l'aménagement écosystémique tout en maintenant les objectifs de la production forestière. Suite à une coupe partielle, les arbres résiduels montrent un taux de croissance radiale et en volume supérieur car ils répondent positivement à une amélioration des conditions environnementales. En principe, pour atteindre une productivité maximale dans les peuplements mixtes de tremble-épinette-sapin, les tiges dominantes de tremble doivent être récoltées en premier afin de favoriser la régénération et la croissance des conifères résiduels, particulièrement l'épinette blanche. Une des principales difficultés dans ce contexte est de déterminer la proportion de peuplier faux-tremble à enlever pour libérer les épinettes blanches de la compétition mais aussi à limiter le drageonnement de tremble et minimiser le stress physiologique qui arrive avec des changements de conditions environnementales extrêmes.

L'objectif principal de cette étude est d'évaluer la réaction de la croissance radiale et en volume des épinettes blanches dans les peuplements soumis à des coupes partielles. Nous avons testé quatre traitements de coupe partielle appliqués dans les années 2001-2002 dans des peuplements mixtes tremble-épinette blanche, selon quatre intensités de prélèvement de tremble (0, 50, 65 et 100% de la surface terrière (ST)). Dix ans après les coupes, 72 épinettes représentant trois classes sociales (dominante, co-dominante et supprimée) ont été abattues et des disques récoltés pour fins d'analyses de tiges. La croissance a été analysée en fonction des facteurs suivants: intensité du traitement, temps depuis le traitement, statut social, taux de croissance avant coupe et compétition des arbres voisins. Par rapport aux peuplements témoins, une réaction positive de croissance a été observée seulement suite au prélèvement de 100% du tremble. Comparativement aux arbres témoins, au cours des dix ans suivant les coupes, les taux de croissance radiale et volumétrique ont été supérieurs de 23,5% et 7,1% pour les dominants, 67,7% et 24,1% pour les co-dominants et 115,8% et 65,6% pour les arbres supprimés. Toutes les classes sociales ont répondu positivement au traitement, mais la croissance en volume absolu était supérieure pour les arbres dominants alors que la croissance radiale était similaire pour les trois classes. En termes de croissance relative, les arbres supprimés ont eu la plus grande hausse de croissance cumulative. Par ailleurs, la réaction de croissance après coupe s'est avérée proportionnelle

au taux de croissance avant traitement. En utilisant des variantes d'indices de compétition de Hegyi, nous avons observé que seuls les voisins conifères ont eu un effet négatif sur la croissance des épinettes échantillonnées. Les résultats indiquent que les épinettes blanches sont capables d'accélérer leur taux de croissance après l'enlèvement du tremble dans ces types de peuplements de la forêt boréale mixte et suggèrent que les réactions positives de croissance seraient encore plus grandes si les traitements incluaient l'éclaircie de conifères agrégé et les dominants.

Mots-clés : coupe partielle, épinette blanche (*Picea glauca* (Moench.) Voss), peuplier faux-tremble (*Populus tremuloides* Michx.), forêt boréale mixte, croissance radiale, croissance de volume, classe sociale.

ABSTRACT

Boreal mixedwood stands in the Abitibi-Témiscamingue region of Quebec are often characterized by a dominance of shade intolerant hardwoods, particularly aspen (*Populus tremuloides* Michx.), with shade tolerant softwoods such as balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench.)Voss) distributed throughout the understory and sub-canopy. Intolerant hardwood and softwood species are typically harvested at the same time via CPRS (cutting with protection of regeneration and soils), the predominant harvesting method applied throughout boreal Quebec. Due to differences in the growth dynamics of aspen and the tolerant softwood species, the conifers in these stands are often of small merchantable size classes when the aspen has reached its maximum growth potential and is suitable for harvest. This has led to an interest in the diversification of silvicultural treatments better suited to the structure and dynamics of mixedwood stands. In certain boreal stand conditions, partial harvesting has been promoted as an alternative silvicultural system to CPRS and as a stand-level tool to meet ecosystem management and forest production objectives. Residual trees are expected to exhibit accelerated radial and volume growth following partial harvesting. In theory, to achieve maximum productivity in mixed aspen-spruce-fir stands, dominant aspen stems should be harvested first, to encourage the regeneration and growth of residual conifers, particularly white spruce. One of the major challenges in this context is determining the appropriate proportion of canopy aspen to remove that will release white spruce trees from competition but limit aspen suckering and minimize physiological stress from the extreme changes in environmental conditions.

The purpose of this study is to evaluate radial and volume growth responses of white spruce trees in boreal mixedwood stands subjected to partial harvesting. Treatments consisted of four intensities of aspen removal (0, 50, 65 and 100% basal area (BA)), applied in 2001-2002. Ten years after treatment, 72 white spruce stems representing three social classes (dominant, co-dominant and suppressed) were destructively sampled and subjected to stem analysis using dendroecological techniques. Growth was analyzed as a function of treatment intensity, time since treatment, social status, pre-treatment growth rate and neighbourhood competition. Accelerated radial and volume growth rates were detected only in the 100% aspen BA removal treatment. Compared to control trees, average annual radial and volume increments were, respectively, 23.5% and 7.1% higher for dominant trees, 67.7% and 24.1% higher for co-dominant trees and 115.8% and 65.6% higher for suppressed trees over the 10 years post-treatment. All social status classes responded positively, but absolute volume growth was superior for dominant trees while radial growth was similar for all three classes. Growth response was proportional to pre-treatment growth rate with vigorous, younger trees having highest growth rates post-treatment. Based on variants of Hegyi's competition index, only coniferous neighbours had a negative effect on white spruce growth. Results indicate that white spruce trees are capable of release following aspen overstory removal in boreal mixedwood stand types and suggest that positive growth responses would be even greater if treatments included thinning of crowded conifers and at least partial removal of dominant conifers.

Key words: Partial harvesting, white spruce (*Picea glauca* (Moench.) Voss), trembling aspen (*Populus tremuloides* Michx.), boreal mixedwood forest, radial growth, volume growth, social class.

CHAPTER I

GENERAL INTRODUCTION

1.1 Introduction to boreal mixedwood forests

The boreal forest encompasses 90% of forested lands in Canada (Chen and Popadiouk, 2002; National Forestry Inventory, 2006), spanning the country from British Columbia and the Yukon Territory to Newfoundland (Chen and Popadiouk, 2002; Thompson and Pitt, 2003). From a global perspective, the Canadian boreal forest accounts for 30% of total boreal forest cover and 10% of the world's forested landmass (Natural Resources Canada, 2014). Despite its extent, tree diversity is relatively low and typically consists of vigorous, generalist species of spruce, pine, fir, tamarack, birches and poplars, which are well suited to cool climatic conditions and recurring disturbances (Brassard and Chen, 2006). Although the boreal forest may seem uniformly spread across the country, it is in fact composed of a variety of forest types that vary in response to local climate, topography, soil conditions and disturbances (Thompson and Pitt, 2003; Brassard and Chen, 2006).

Mixedwood forests account for 16% of total forest cover in Canada (Natural Resources Canada, 2014). Boreal mixedwood forests are comprised of both deciduous and coniferous species and are often representative of forests transitioning from hardwood to softwood dominance. In Quebec, a stand is considered to be mixed when it contains both conifer and broadleaf species, without one species type accounting for more than 75% of the total stand basal area (MRNF, 2009). In the Abitibi-Témiscamingue region of north-western Quebec, boreal mixedwood forests are found in the western Black spruce (*Picea mariana* (Mill.) BSP) - feathermoss and in the Balsam fir (*Abies balsamea* (L.) Mill.) - white birch (*Betula papyrifera* (Marsh.)) bioclimatic subdomains (Saucier, 1998). In this region, mixedwood stands are initiated following large scale disturbances and often represent mid-successional stages of development (Bergeron and Harvey, 1997). Shade intolerant hardwoods, such as aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and white birch

typically initially dominate forest canopy on mesic sites, with shade tolerant conifers including white spruce (*Picea glauca* (Moench.)Voss), black spruce and balsam fir in the understory. The structure and composition of these stands greatly depends on species traits, particularly modes of regeneration, initial growth rates, shade tolerance and longevity, as well pre disturbance stand conditions and the nature of the disturbance. Depending on the stage of stand development, species composition and partial disturbances, the softwood component may co-dominate the stand or may be temporarily restricted to the understory. In comparison with other boreal forest types such jack pine (*Pinus banksiana* Lamb.) stands on dry, sandy soils or lowland black spruce forests, boreal mixedwoods are associated with mesic sites and considered relatively complex ecosystems that support a broad diversity of floral, faunal and fungal species (Chávez and Macdonald, 2012). The high productivity of mixedwood stands make them important ecologically for maintaining biodiversity, wildlife habitat, biogeochemical cycling and carbon sequestration (MacDonald, 1995; Thompson and Pitt, 2003; Brassard and Chen, 2006).

Forest management has intensified over the last half century, particularly with the modernization of harvesting equipment and with increasing global demand for wood products (Comeau et al., 2005). Conifer species, especially white and black spruce, have always had higher economic value than intolerant hardwood species. Canada is the leading exporter of softwood lumber and pulp and paper products, which account for approximately 12 billion dollars in annual revenue (Natural Resources Canada, 2014). In the past, intolerant hardwood-dominated mixed stands have generally been avoided, primarily because of the low commercial value of the hardwood component (and thus greater softwood wood procurement costs) and because the conifer component may often be of small or pre-mature size classes. However, in many boreal regions, harvesting of conifer-dominated mixedwoods followed by inadequate conifer regeneration and vegetation control has resulted in substantial increases in the proportion of intolerant hardwood-dominated mixedwood forests to the detriment of softwood-dominated forest (Grondin and Cimon, 2003). Consequently, it is expected that the forestry industry will become increasingly reliant on boreal mixedwood stands, even those with a strong hardwood component, to meet their wood supply needs.

In recent decades, the economic importance of intolerant hardwoods has increased with advancements in wood processing technologies and growing market opportunities (Natural Resources Canada, 2014). In particular, aspen is the primary constituent in the manufacture of oriented strand board (OSB), which has virtually replaced plywood in most Canadian and US housing construction. While the utilization and exportation of intolerant hardwood products remains relatively low compared to softwood products across the country (Natural Resources Canada, 2014), aspen, and to a lesser extent balsam poplar and birch, are used in the production of OSB and laminated veneer lumber (LVL) in mills in the Abitibi-Témiscamingue region.

Despite their respective commercial possibilities, when white spruce and aspen cohabitate in mixedwood stands, their inherent differences in regeneration and growth dynamics make it difficult to maximize total stand yield using a single harvest treatment. The initially slower growing white spruce trees are often in pre-commercial or small merchantable size classes when the faster growing aspen have reached their peak growth (Chen and Popadiouk. 2002). The differences in height and diameter growth between the two species are related to their respective growth potentials as well as their capacity for increased growth during periods of reduced competition (Claveau et al., 2002; Filipescu and Comeau, 2007). White spruce is generally suppressed by the initially faster growing aspen, but often experiences periods of accelerated growth coinciding with periods of reduced growth in aspen, including senescence (Bergeron and Charron, 1994). Thus, when white spruce trees are suitable for harvesting, the aspen trees have often already passed their maximum growth period and are in physiological decline. Normally, using clear-cutting or harvesting with protection of advance regeneration and soils (CPRS), both species would be harvested at the same time. This ultimately results in losses of either aspen or white spruce volume, since the two species do not attain maximum growth rates at the same point in time (MacDonald, 1995). In this regard, the development of alternative silvicultural approaches better suited to the structure and dynamics of boreal mixedwoods constitute an opportunity to maximize stand productivity and possibly enhance white spruce regeneration. Such approaches should be based on well designed and documented silvicultural experiments and will require a thorough understanding of mixedwood dynamics and the use of innovative harvesting techniques.

1.2 Stand structure, composition and dynamics

Stand structure refers to the vertical and horizontal organization of living and dead trees from leaf litter and woody debris on the forest floor, into the understorey and up through to the top of the canopy (McElhinny et al., 2005). Stand complexity is defined by the arrangement of the stand structure, the component species, the number of individuals and interactions between the biotic and abiotic environments. Ecological processes such as seedling and sapling recruitment, competition, mortality, decomposition and nutrient cycling as well as soil productivity and natural disturbances are important factors in determining the spatial patterns of tree colonization, growth and survival (Chen and Popadiouk, 2002; Brassard and Chen, 2006). Species traits such as longevity, reproduction, nutrient requirements and shade tolerance are also important factors in influencing how a forest stand will develop (Bergeron, 2000; Chen and Popadiouk, 2002). A number of studies have led to a good understanding of successional dynamics in the boreal mixedwood forests of northwestern Quebec composed of aspen, balsam fir and white spruce (Bergeron and Charron, 1994; Bergeron and Harvey, 1997; Kneeshaw and Bergeron, 1998; Bergeron, 2000; Pothier et al., 2004). Over time, natural succession brings about changes in the stand structure and composition of boreal mixedwood forests, generally involving a decrease in the proportion of short-lived, shade-intolerant hardwood species in favour of an increased proportion of more shade-tolerant and, with the exception of balsam fir, more long-lived conifer species (Brassard and Chen, 2006).

1.2.1 Stand initiation

The stand initiation phase occurs following a severe disturbance such as a natural fire or harvesting where the majority of mature trees are killed, and in the case of harvesting, removed. Canopy removal creates new growing space and favourable environmental conditions allowing for the colonization of an initial cohort of pioneer tree species. The type and severity of the disturbance along with site and stand conditions prior to disturbance will strongly influence the initial post-disturbance species composition. Aspen's capacity to root sucker is well adapted to stand initiating disturbances and open conditions therefore, it is often the primary early successional tree species on rich, mesic sites, typical of the claybelt

region of northwestern Quebec and northeastern Ontario (Bergeron, 2000; Chen and Popadiouk, 2002). Furthermore, since suckering occurs locally, within the limits of parent root systems, aspen is more likely to dominate site colonization if it was present on the site prior to the disturbance. An initial cohort of aspen can establish quickly and reach very high densities of tens of thousands of stems per hectare because of the species adaptations for efficient growth in high light conditions and its ability to regenerate vegetatively (Brais et al., 2004; Groot et al., 2009; Prévost and DeBlois, 2014). According to Pothier et al. (2004), aspen growth decline occurs, on average, around 60-65 years of age but the timing varies greatly, depending on site, climate and genetic factors. Moreover, aspen suckering may give way to the development of multiple cohorts which can dominate a stand for over 100 years (Bergeron and Dubuc, 1988; Cumming et al., 2000). White spruce cannot vegetatively regenerate and thus relies on seed sources for establishment following a major disturbance. White spruce establishment therefore depends on an abundant seed crop as well as favourable germination sites (Greene et al., 1999; Martin-DeMoor et al., 2010; Robert et al., 2012). The stand initiation phase concludes with the closing of the aspen canopy.

1.2.2 Stem exclusion

The stem exclusion phase begins when the dominant aspen have experienced rapid lateral growth preventing new trees from occupying the canopy. Intense competition for light combined with finite growing space results in a dramatic reduction in stem density of aspen in a relatively short period of time (Chen and Popadiouk, 2002). Suckering is inhibited as the amount of sunlight that is able to penetrate the forest floor is diminished. The opposite is true for spruce and balsam fir, where stem densities have been shown to increase during the period of aspen self-thinning (Chen and Popadiouk, 2002). Compared to aspen, white spruce generally establishes more gradually in the stand and slow juvenile growth limits saplings to the aspen understorey for several years (Bergeron and Charron, 1994; Harvey et al., 2002) until they outcompete other vegetation in the shrub layer (Groot, 1999; Chen and Popadiouk, 2002). This results in a vertical stratification of trees and the development of mixedwood stands, as the heavy shade in the understorey limits suckering and sucker survival but not necessarily establishment and growth of the more shade-tolerant conifers.

1.2.3 Canopy transition

Canopy mortality of the initial aspen cohort eventually shifts from being density-dependant to density-independent (e.g., associated with natural senescence, fungal infection). At this point, stand breakup begins to occur (Pothier et al., 2004) freeing up growing space, light and nutrient resources. When tolerant conifers are already present in the understory or sub-canopy, progressive mortality of overstory aspen eventually leads to their replacement by balsam fir, white and black spruce as stands slowly transition toward conifer dominance (Harvey et al., 2002). Intermediate and understorey white spruce trees and other conifers frequently experience accelerated diameter and height growth as they are released from competition. This period of high growth has been found to correspond with relatively slower rates of growth of the deciduous component (Bergeron and Charron, 1994). The canopy transition period can be accelerated or delayed by small or partial disturbances such as insect outbreaks or senescence and mortality of individual trees. Again, when conifers are present in the understory, an outbreak of forest tent caterpillar (*Malacosoma disstria*), for example, can accelerate the transition by causing mortality of some or all aspen (Gendreau-Berthiaume et al., 2012). However, Moulinier et al. (2011) showed that, if conifers are absent, the same outbreak can have the opposite effect; that is, site occupation of aspen will be prolonged because canopy opening will stimulate sucker recruitment. Spruce budworm (*Choristoneura fumiferana*) outbreaks can induce retroaction in stand succession dynamics, by causing severe foliage and growth loss and mortality of host species (fir and spruce), thereby improving understorey conditions, particularly light levels, for regeneration and growth of intolerant hardwoods that recruit into gaps (Kneeshaw and Bergeron, 1998).

1.2.4 Gap dynamics

Where the time between stand replacing disturbances is longer than the lifespan of the initial cohort of pioneer hardwood species, small gaps in the canopy start to appear as individual or groups of individual trees die (Kneeshaw and Bergeron, 1998; Chen and Popadiouk, 2002). Regeneration in the gaps create an uneven canopy with a patchy arrangement of young, intermediate, old and dying trees throughout the stand. The layout of the dead trees is important for the growth and re-establishment of the understory trees. Standing trees that

perish slowly over time, are important for the release of advance regeneration whereas uprooted trees, for example resulting from windthrow, create suitable substrates for seedling establishment (Lieffers et al., 1996; Robert et al., 2012). The decomposing fallen trees as well as exposed mineral soil provide two of the best seedbeds for white spruce recruitment. This is because of reduced competition with herbaceous plants and shrubs, the lack of leaf debris which typically inhibits root penetration into the soil and because rotting wood maintains a humid environment which is essential for the survival of small germinants (Robert et al., 2012). Gap size is an important factor influencing recruitment in mixedwood stands (Kneeshaw and Bergeron, 1998; Beaudet et al., 2011), in that larger gaps provide more sunlight exposure, thus tending to favour regeneration and growth of aspen and white birch whereas smaller gaps tend to favour regeneration of more shade-tolerant conifers. These species generally grow well in diffuse sunlight, and are more prone to water and heat stress which can occur in larger gaps (Callaway, 1995; Kneeshaw and Bergeron, 1998). Maintenance of mixedwood stands therefore depends on reoccurring small scale disturbances, site conditions and the traits of the species involved (Bergeron and Harvey, 1997; Man and Lieffers, 1999a).

1.3 Tree growth

Reliable measurements of tree growth are essential for assessing the effects of silvicultural treatments as well as predicting future wood yields (Avery and Burkhart, 2002). Although growth predictions are typically calculated at the stand-level, it is first necessary to analyze growth at the tree level, since it is a fundamental component of stand level production (Avery and Burkhart, 2002).

Tree growth is an irreversible and periodic processes represented by an increase in volume resulting from the formation of new cells, their enlargement and differentiation into different growing parts (Vaganov et al., 2006). The seasonal period of growth depends on annual fluctuations in environmental conditions (Vaganov et al., 2006) during which time growth may occur simultaneously or independently in different parts of the tree. Growth increment refers to the change in size between the beginning and end of a growth period and can be measured by several parameters including the change in radius, diameter, basal area, height

or volume. Growth is influenced by internal factors including species genetics as well as tree age and by the external environment in which the tree is situated. External influences include climatic conditions such as temperature, precipitation, wind and sunlight; soil conditions include moisture, texture and chemical characteristics; and physio-geographical conditions like slope, elevation and aspect (Vaganov et al., 2006). Complete tree growth involves the extension and thickening of the shoots, stems and roots.

Under natural growing conditions, growth curves for diameter, basal area, height and volume generally follow a similar elongated sigmoidal shaped pattern as a function of age (Assmann, 1970). In juvenile years, growth in all dimensions is typically slow until the seedling becomes well established (Avery and Burkhart, 2002). As the tree matures, it enters the full vigor stage, during which time it experiences a rapid increase in growth (Assmann, 1970). Once the growth rate has peaked, it declines slowly during the senescence phase (Assmann, 1970). As long as the tree is living and healthy it will continue to grow, though the magnitude of growth may be severely reduced (Avery and Burkhart, 2002).

Primary growth involves the lengthening of shoots and roots through apical meristems where high cell division contributes to the vertical extension of the tree (Raven et al., 2005). Root extension anchors the tree and increases its surface area, which is important for water and nutrient absorption from the soil (Raven et al., 2005). Shoot extension occurs at the tip of the stem resulting in height growth. Secondary growth is initiated by lateral meristems, or cambium, and results in the thickening (increase in diameter) of the stem and roots (Raven et al., 2005). The cambium layer perpetually produces an unlimited number of cell divisions that differentiate into secondary tissues (Raven et al., 2005). Cells formed on the outside of the cambium layer will differentiate into phloem which is primarily responsible for photosynthate transportation along the length of the stem (Raven et al., 2005). Cells formed on the inside of the cambium layer will differentiate into xylem tissue, which in conifers is mainly composed of tracheid cells, the primary component of wood, and is responsible for water transport throughout the stem (Raven et al., 2005). Throughout the growing season the xylem matures by undergoing a series of growth phases that involve radial expansion of the tracheids and thickening of the cell wall (Vaganov et al., 2006). The seasonal periodic activity of these growth processes results in the formation of annual growth rings which are

made visible by the difference in colour and structure of the earlywood and latewood (Vaganov et al., 2006). Earlywood is produced at the beginning of the growing season and is characterised by its lighter colour, larger radial cell size, thinner cell wall and lower density (Vaganov et al., 2006). In mid growing season, the structure of the tracheids transitions into the formation of latewood. Latewood is characterised by its darker colour, smaller radial cell size, thicker cell wall and higher density (Vaganov et al., 2006). Density is the most important factor influencing wood quality (Kennedy, 1995). For spruce, annual rings closest to the pith typically exhibit the highest density, followed by a gradual decrease and minimum density usually reached in the first 20 years of growth (Kennedy, 1995; Gagné et al., 2012). Wood density then increases to an intermediate level in later years (Kennedy, 1995; Gagné et al., 2012).

It is necessary to differentiate the age of the tree as a whole from the age of tree tissue, particularly the cambial age. While the actual age of the tree is the cumulative number of years since establishment, cambial age is based on the year of ring formation. Since new sheaths of tissue are layered on annually over the length of the stem, the cambial age at the top of the tree is younger relative to cambial age at the base of the tree. Cambial age is determined by counting the number of rings at any given height of a tree. Young cambium is highly active, resulting in greater wood production and thicker annual rings than those produced by older cambium (Vaganov et al., 2006).

Among other factors, height growth is influenced by a species' shade tolerance. Species that require high light levels, like aspen, generally reach their maximum annual increment earlier than more shade tolerant species, like white spruce. On rich sites, height growth is rapid during the full vigor stage, until the tree reaches an age of culmination during which time height growth rate decreases and its cumulative height is maintained into senescence (Assmann, 1970). Intense neighbourhood competition during the early years restricts height growth of saplings and seedlings, resulting in vertical stratification of height classes. The relative position of a tree, referred to as its social status, consists of the tallest trees or dominants which have well developed crowns and dominate the canopy; co-dominant trees which have relatively normal crowns but are more weakly developed than the dominants; and

intermediate and suppressed trees which have stunted crowns and primarily occupy the middle-understory layers (Assmann, 1970).

In dense stands, radial growth of white spruce – as with other species - is more strongly affected by competition than height growth (McClain et al., 1994). Once respiration demands of a tree have been met, allocation of carbon is prioritized to height growth in an attempt to maintain or better its social ranking in the stand (Wagner, 2000). As more resources are available in less dense stands, a greater proportion of photosynthate becomes available for diameter growth (McClain et al., 1994). At any given height along the stem, radial increment is greatest near the pith where cambium age is young, reaching maximum growth rate within the first few years then gradually declining towards the bark with increasing cambium age (Vaganov et al., 2006). Longitudinally, the stem profile for a typical spruce tree follows a growth pattern where growth is greatest in the butt, decreases in diameter increment towards the base of the crown and then increases again before thinning towards the tip of the tree (Assmann, 1970; Clyde and Titus, 1987). This pattern is most evident for middle aged trees and becomes less exaggerated as tree age when height increment is reduced and diameter increment becomes more evenly distributed along the length of the stem (Clyde and Titus, 1987).

Radial growth in white spruce is also strongly related to crown length, as growth is highest in areas with greater leaf biomass and photosynthetic activity. In dense stands where light levels decrease steeply between the upper and lower canopy, photosynthesis becomes less efficient in lower branches and crown recession occurs as trees self-prune (Power et al., 2012). As a result, stems become more cylindrical in form as the branch free region of the bole becomes progressively longer and diameter increment is reduced (Mäkinen and Isomäki, 2004). When stand density is low or reduced through silvicultural treatments, for example, trees tend to maintain their lower branches and therefore have longer crowns; as a result, diameter growth remains high in lower parts of the bole. Furthermore, stronger wind speeds in more open stands causes bending stress in trees. In these conditions, diameter growth becomes unequally distributed, as increased growth is allocated to stressed parts, particularly at the base of the stem; to improve anchorage, trees will also invest in root growth (Urban et al., 1994; Kneeshaw et al., 2002). Trees grown in less dense stands therefore tend to have more of a

conical than cylindrical stem form. Stem taper, an important measure of tree value, is the gradual decrease in diameter from the base to the tip of a tree over the length of the stem. Because the cylindrical form produces maximum wood recovery for the sawmill industry, trees with high stem taper typically have lower economic value and often exhibit poor wood quality characteristics (Tong and Zhang, 2008). The intermediate shade tolerance and typical long crown length of white spruce favour a larger diameter increment over time, compared to other intolerant conifer species such as pines (Clyde and Titus, 1987).

1.4 Silvicultural practices in boreal mixedwood forests

1.4.1 Traditional harvesting practices

With increased industrial utilization of aspen, mixedwood forests have become an important source of both hardwood and softwood volumes for the Canadian forest industry (Comeau et al., 2005; Pitt et al., 2010). Silvicultural practice following clear-cutting or careful logging regimes have generally promoted successive rotations of similarly composed stands of either intolerant hardwoods by exploiting the prolific natural regeneration of aspen, or softwoods by relying on site preparation, planting and vegetation competition control. This reduction of stand and forest-level compositional and structural complexity has been referred to as "unmixing the mixedwoods" (Bergeron and Harvey, 1997; Pitt et al., 2010). Clear-cutting can be a very effective treatment for initiating virtually pure stands of aspen; however, when the objective after harvesting is to regenerate pure spruce stands, intensive management interventions are generally required to minimize the effects of competition and establish early spruce dominance (Groot, 1999; Man et al., 2008; Pitt et al., 2010).

The predominant harvesting method applied throughout Quebec is CPRS, where all merchantable stems ≥10 cm in diameter at breast height (DBH) are felled. CPRS aims to protect advanced regeneration and minimize soil disturbance by restricting harvesting equipment to parallel skid trails that cannot exceed more than 25% of cutover area. Ostensibly, the objective of CPRS is to regenerate the forest naturally from advance regeneration or vegetative propagules, and in this regard, it differs from clear-cutting.

However, to most forest users, it resembles a variant of clear-cutting and like clear-cutting, there has been growing public and scientific criticism over the generalized (over)use of CPRS, particularly some of its pernicious effects. Most notably, the unprecedented rate of loss of old and over-mature forests and, in some cases, by not disturbing soils enough, favouring balsam fir regeneration over spruce (Harvey and Brais, 2002) or resulting in decreases in forest productivity (Lafleur et al., 2010). Extensive forest harvesting followed by inadequate regeneration practices over the last half century have reduced the abundance softwood dominated stands in mixedwood regions (balsam fir - white birch and balsam fir - yellow birch bioclimatic domains in Quebec), augmenting the proportion of mixedwood stand types and placing greater reliance on these mixedwood stands to meet demands for spruce lumber (Yang, 1991).

Due to differences between aspen and white spruce in terms of regeneration, tree growth rate and shade tolerance, aspen attains canopy dominance when the white spruce are still generally of small commercial size in the sub-canopy and understory. Harvesting both species at the same time, using CPRS or a similar harvesting method, would therefore appear to result in a loss in stand productivity, since the softwood component is harvested before it has attained its full growth potential (MacDonald, 1995). In contrast, protecting and retaining the immature and understorey conifer trees while harvesting the aspen component could 1) permit spruce stems to continue to accrue volume, 2) shorten the following rotation cycle, and 3) eliminate or reduce the costs associated with white spruce regeneration and tending (Man et al., 2008). According to Thompson and Pitt (2003), silvicultural techniques that promote the regeneration and growth of valuable conifer species, such as the approach mentioned, should be a priority for the forest industry.

1.4.2 Forest ecosystem management

The legal and regulatory framework governing forest management practices in Quebec has undergone several revisions in the last three decades, the most recent being the Sustainable Forest Development Act which was put into force in April 2013. The Act is intended to ensure sustainable development of the province's forest resources for environmental, economic and social purposes (Quebec, 2010). Over the past two decades, an ecosystem-

inspired management paradigm, also referred to as forest ecosystem management (FEM), has emerged with the fundamental principle of maintaining long-term ecosystem viability (Attiwill, 1994; Galindo-Leal and Bunnell, 1995; Bergeron and Harvey, 1997), and is central to Quebec's new sustainable forest policy. To ensure long-term ecological viability of managed forests, FEM aims to maintain forest ecosystem health and resiliency by reducing the major differences between managed and natural forest landscapes (Gauthier et al., 2009). Theoretically, this approach also ensures the maintenance of habitats critical to a multitude of floral and faunal species thus, to a certain degree, sustaining biological diversity (Gauthier et al., 2009).

Advances in ecological knowledge have led to a better understanding of the natural dynamics of boreal mixedwoods (Chen and Popadiouk, 2002; Jardon et al., 2003; Bergeron et al., 2004) and natural disturbances are now clearly recognized as important drivers in the long-term functioning and regulation of forest ecosystems (Attiwill, 1994). A fundamental principle of FEM is to fully integrate knowledge and understanding of natural forest dynamics into management practices at stand, landscape and regional levels in order to maintain key ecological attributes and processes of natural forests, including those which are influenced by or result from natural perturbations (Attiwill, 1994; Vaillancourt et al., 2009; Patry et al., 2013). At the landscape level, management objectives should aim to maintain the necessary proportion of early, mid and late successional stages of forests with spatial organization, distribution and connectivity within the range of natural variability (Bergeron et al., 1999, Landres et al., 1999).

At the stand level, objectives should focus on maintaining stands of a variety of forest types, with compositional and structural complexities as inspired by the outcomes of natural disturbances and stand dynamics (Attiwill, 1994). Forest ecosystem-based management does not aim to mimic natural disturbance or eliminate even-aged harvesting treatments, such as CPRS. Rather, FEM silvicultural practices are intended to ameliorate or adapt conventional practices to better maintain features of natural forests within managed forest landscapes. It is thought that this can be achieved by diversifying silvicultural practices which vary in intensity, pattern and spatial scope (Harvey et al., 2002). Because the boreal forest has been overwhelmingly managed under an even-aged regime which, arguably, reduces ecosystem-

level diversity, treatments that emulate natural partial disturbances have been promoted to counter this effect by generating greater stand and, cumulatively, forest-level diversity (Bergeron and Harvey, 1997; Harvey et al., 2002).

Despite a good understanding of aspen-conifer dynamics in the boreal mixedwoods, adaptive silvicultural treatments that better exploit both hardwood and softwood components for the forest industry while maintaining ecosystem functions are still in development (Brais et al., 2004; Prévost et al., 2010). While several ecosystem-inspired management practices have been incorporated into forest regulations in several Canadian provinces, their effective implementation and measurement of success can be difficult due to the inherently complexity of boreal mixedwood stands (Thompson and Pitt, 2003) and the time horizons involved.

1.4.3 Partial harvesting

Partial harvesting has been promoted as an ecosystem-inspired silvicultural treatment (or rather, category of treatments), with the idea that it has the potential to maintain ecosystem services and the compositional and structural attributes of natural forests while also meeting other silvicultural objectives such as sustained wood production (Comeau et al., 2005). Partial harvesting is a generic term and is defined here as a commercial, stand-level silvicultural treatment in which a portion of canopy trees are harvested. In this sense, partial harvesting covers a broad spectrum of cutting intensities and configurations, with the common element that not all commercial-sized trees are harvested in a partial cut. Moreover, partial harvesting differs from variable retention (VR) in that residual trees in VR are left as biological legacies permanently, or at least for a full rotation (Gustafsson et al., 2012), whereas in the case of partial harvesting, all or a portion of residual stems are intended to be harvested during a later stand entry.

Theoretically, partial harvesting treatments simulate low-intensity, secondary disturbance processes, such as insect outbreaks, local windthrow or mortality due to competition or senescence, that would naturally result in some tree mortality and canopy gaps (Harvey et al., 2002). One argument for applying partial harvesting treatments in aspen-conifer mixedwood stands is that selective removal of aspen stems simulates, to some extent, the natural

successional process of aspen mortality in the transitional phase of stand development. Moreover, a redistribution of light and nutrient resources via the partial removal of the aspen overstory (Man and Lieffers, 1999; Filipescu and Comeau, 2007) should "release" the residual conifer stems from competition, resulting in an acceleration of diameter, height and volume growth. Clearly, there exists a silvicultural argument for applying partial harvesting treatments in these mixed stands and it is likely that they will be increasingly applied in northwestern Quebec and other parts of the boreal forest as ecosystem management regulations and guidelines are implemented. While there are numerous potential benefits to partial harvesting in boreal mixedwood stands, these must be weighed against economic and operational constraints to determine their feasibility and potential for success (Table 1).

Table 1.1 Potential benefits and constraints to partial harvesting in boreal mixedwood forests

1. Potential benefits
Contributes to meeting forest ecosystem management goals
More residual forest cover than following CPRS
Greater compositional & structural complexity than CPRS
Better residual habitat of intact forest than CPRS
Lower impacts on wildlife habitat, biodiversity
Increased forest productivity by synchronizing harvesting with growth potential of component species
Greater protection of regeneration, sapling and tree layers
Reduced vegetation competition and enhanced conifer (spruce) establishment
Maintenance of local seed source (residual trees, particularly white spruce)
In stands containing white spruce, can contribute to maintaining white spruce and reduce the relative proportion of balsam fir
Favours future growth potential of pre-mature and small merchantable residual stems, including white spruce, following treatment
Bigger stems = easier and cheaper processing in forest and mills; higher product value
Public perception - greater social acceptability than clear-cutting
2. Constraints
Requires specialized equipment
High stem density restricts movement of machinery
Potential logging damage to residual stems
Potential for significant mortality of residual stems (volume loss)
Possible growth lag of residual stems
Removes less volume/area - requires greater harvest area to meet volume objectives
Higher economic costs associated with planning, road construction and maintenance, harvesting, monitoring
Uncertainty concerning yields, stand stability, survival, stand renewal, etc. - few long-term studies measuring success
Potential negative effect on wood quality

1.5 Tree growth responses to partial harvesting

There are several internal and external factors that can affect growth responses of trees to partial stand removal and, in many cases, these factors are augmented through the application of silvicultural treatments such as partial harvesting. It has long been recognized that smaller and younger trees have a strong capacity to respond positively in terms of improved radial and volume growth following release from competition, a tendency that has formed the basis of commercial thinning practices. Several recent studies have, however, reported that mature residual trees are also capable of responding positively to release treatments. When neighbouring trees are removed through partial harvesting, residual trees typically exhibit increased growth rates above pre-treatment levels.

For example, following an initial seed cut of a regular shelterwood system in a 174 year old, nearly pure white spruce stand in Alaska, Youngblood (1991) determined that dominant and co-dominant white spruce trees exhibited superior radial growth rates compared to pre-treatment levels. On average, radial growth increased 27% per year, resulting in a net mean increase in diameter growth of 164%, over a period of 8 years post-treatment. This growth acceleration was attributed to the thinning treatment which removed 66% total stand BA. This partial harvest was designed to encourage white spruce regeneration by creating favourable seed beds and leaving 100 dominant and co-dominant seed trees, equally spaced 9 to 12 m apart.

In mixedwood stands in Manitoba, Yang (1989) tested the effect of two thinning intensities concentrating on aspen overstory removal, on the growth responses of residual white spruce trees. Treatments consisted of a relatively light thinning corresponding to 44% stand BA removal and a moderate thinning of 60% BA removal. Fifty years post-treatment, diameter and volume increments showed 28% and 81% and 50% and 260% improvement for the light and moderate thinnings, respectively, when compared to trees in control stands. In the same study, for similarly composed mixedwood sites situated in Saskatchewan, Yang (1989) found that when subjected to complete aspen removal, white spruce diameter increment improved 50-177% while volume increment improved 24-304% compared to control trees over a period of 35 years.

Similarly, in stands ranging from 5-65 years in Alberta, Yang (1991) observed improved growth rates of white spruce when direct aspen neighbours within a circular area two times the crown radius were removed and herbicide treatments applied to aspen stumps. Residual trees showed 41% improvement in diameter growth and 82% increase in volume growth compared to control trees over a post-treatment period of 35 years.

Statistical analysis of models developed using metadata derived from several independent white spruce studies throughout western Canada and parts of the USA, support the conclusion that residual trees display accelerated diameter, height and volume growth rates relative to controls following a range of partial harvesting treatments (Man and Greenway, 2004).

Other conifer species have also shown similar patterns of enhanced growth following release. In lowland black spruce stands in northern Ontario, Thorpe et al. (2007) found that residual black spruce trees subjected to HARP (Harvest with Advance Regeneration Protection, similar to CPPTM, *coupe avec protection de petites tiges marchandes*), which reduced stand BA by 80% by concentrating removal of larger size classes (>14 cm DBH), resulted in accelerated radial growth during the 12 year post-treatment period. Radial growth peaked 8 to 9 years post-treatment, at which time radial growth was double the mean pre-treatment level (mean radial growth rose from 0.54 to 1.10 $mm \cdot year^{-1}$).

In central Ontario, diameter growth rates for white pine (*Pinus strobus*) have been observed to increase by 60% in stands subjected to retention harvesting of 50% white pine BA (approximately 24% of total stand BA removal). Treatments were designed to maintain structural heterogeneity and age structure of the stands by leaving both vigorous seed trees and trees in declining health which would eventually contribute to snags and coarse woody debris (Bebber et al., 2004).

Furthermore, in mixed stands in the Great Lakes-St. Lawrence Forest Region of the Petawawa Research Forest in eastern Ontario, Bevilacqua et al. (2005) established that white pine experienced accelerated growth rates following partial harvesting, and that growth response depended on tree social status. Compared to control trees, average annual diameter

and volume increments were, respectively, 63% and 35% higher for dominant trees, 62% and 43% higher for co-dominant trees and 231% and 170% higher for suppressed trees over the 23 years post-treatment.

In mixed stands in the balsam fir -yellow birch bioclimatic domain of Quebec, Gendreau-Berthiaume et al. (2012) evaluated two partial harvesting treatments that predominantly removed intolerant hardwood species and balsam fir, and compared them to stands that had been affected by partial natural disturbances (windthrow and forest tend caterpillar). Trees were harvested along 5 m wide skid trails, separated by 15 m wide residual bands. Two treatment intensities were tested. The first termed a "successional cut" where all balsam fir (>10 cm DBH), 2/3 intolerant hardwood trees (>10 cm DBH), and some spruce (>24 cm DBH) were removed, resulting in 47.9% total BA removal. The second treatment termed "diameter limit" where all balsam fir and intolerant hardwood trees (>10 cm DBH), and some spruce (>18 cm DBH) were removed, resulting in 63.2% total BA removal. After 4 years post-treatment, total stand BA increased by 25 and 13.5% in the succession cut and diameter limit cut, respectively, compared with the naturally disturbed stand in which the BA was relatively stable over the 4 years. Additionally, white birch, balsam fir and white spruce showed the highest increases in BA relative to initial levels, indicating that these species have the capacity to respond positively to partial harvesting treatments.

In the Pacific Northwest, Latham and Tappeiner (2002), found that although growth responses to partial harvesting were slow and occurred over a period of 20 years, very old ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) trees did display increased growth rates and improved vigor over controls.

Partial harvesting treatments have also been shown to improve recruitment of conifer seedlings and increase growth of advanced growth and large saplings (Man et al., 2008; Gendreau-Berthiaume et al., 2012). Growth responses to partial disturbances can be highly variable among trees even for the same species, possibly due to differences in age and size or to local resource availability and neighbouring competition (Thorpe et al., 2007). Results of Youngblood (1991), Thorpe et al. (2007) and Latham and Tappeiner (2002), suggest that

large mature trees are capable of responding to release from competition induced by partial harvesting treatments.

One trend that has been frequently observed among different conifer species is a time lag in growth responses following partial harvesting treatments. Reports of response lag in white spruce are variable: improved growth rates have been reported to occur immediately following treatment (Man and Greenway, 2004), after two years (Youngblood, 1991), and up to nine years post-treatment (Urban et al., 1994). Time lags have also been observed in black spruce (Thorpe et al., 2007; Gendreau-Berthiaume et al., 2012), white pine (Bebber et al., 2004), Douglas fir and lodgepole pine (*Pinus contorta*) (Kneeshaw et al., 2002). These delays in stem growth response have been attributed to growth allocation to other parts of the tree, particularly roots, which is thought to increase stability against windthrow (Urban et al., 1994) and offset the transpiration losses associated with environmental changes, particularly greater radiation and wind exposure (Kneeshaw et al., 2002). The time period in which residual trees reach their peak growth rate and maintain an accelerated growth response over pre-treatment levels is also highly variable among species and treatments. Growth declines following initial increases have been reported as early as nine years post-treatment for black spruce to decades in white spruce and other conifer species (Youngblood, 1991; Latham and Tappeiner, 2002; Thorpe et al., 2007).

1.6 Treatment intensity

The total or partial removal of aspen in mixed stands has the potential to shorten the canopy transition phase from hardwood to softwood dominance (Bergeron and Harvey, 1997) and partial harvesting has been suggested as an option for converting even-aged (or even-sized) stands to uneven-aged and sized mixed stands, with the objective of restoring forest complexity and the characteristics of natural mixedwoods (Nyland, 2003). In the context of ecosystem management, partial harvesting reduces the differences between naturally disturbed and developing forests and those under management by maintaining forest cover with mixed species compositions in multiple age and size classes (Man et al., 2008; Gendreau-Berthiaume et al., 2012). These attributes are important for the maintenance of structural complexity, considered important for wildlife habitat, biodiversity and ecosystem

resilience (Chen and Popadiouk, 2002; McElhinny et al., 2005). Furthermore, the residual forest cover provides seed source for natural seedling recruitment and a tempered environment for advanced regeneration while generally reducing the intensity of aspen recruitment (Brais et al., 2004; Prévost and DeBlois, 2014).

One of the challenges for forest managers has been to determine the appropriate amount of canopy opening that will maintain enough cover to suppress competition from shade intolerant herbaceous, shrub and aspen regeneration but allow for an adequate amount of sunlight for the growth of understorey white spruce (Comeau et al., 2005). Aspen suckering has been found to increase proportionally to partial harvesting intensity (Prévost and Pothier, 2003; Brais et al., 2004) and, due to its fast growth rate, has the potential to repress seedlings and saplings and limit the growth of juvenile white spruce and other conifers. Understorey conifer regeneration and growth have also been found to increase proportionally with partial harvesting intensity (Prévost and Pothier, 2003). Excessive removal of canopy trees can however have a negative impact on residual trees by causing physiological shock related to wind, water and heat stress, and thereby postponing growth responses and limiting diameter growth (Prévost et al., 2010). A partial harvesting intensity of 45 to 65% total basal area removal has been suggested as optimal, as it provides a compromise between adequately limiting aspen suckering and other herbaceous competition and maximizing white spruce growth response (Prévost and Pothier, 2003; Prévost et al., 2010; Beaudet et al., 2011). It is clear that harvesting intensity will have an influence on the growth responses of residual trees. On rich sites, however, grasses such as *Calamagrostis canadensis or* shade tolerant woody shrubs such as mountain maple (*Acer spicatum*) that are present in the understory may also come into play in post-treatment dynamics (Lieffers and Stadt, 1994; Bose et al., 2014).

1.7 Neighbourhood environment and competition

The growth and survival of an individual tree depends its ability to capture available light, water, soil nutrients and growing space. When the demand for these resources is higher than the supply, competition occurs between neighbouring individuals (Balandier et al., 2006). Interspecific competition ensues when one individual has a negative effect on the growth of another individual. Once trees have attained the "free-to-grow" stage, grasses, herbs and

shrubs are considered to be strong competitors for belowground water and soil nutrient resources, whereas canopy trees are stronger competitors for growing space and light resources (Balandier et al., 2006). Each tree is limited by the amount of space above and below ground in which it has to grow and this can be restricted by the number and proximity of neighbours. Neighbourhood competition indices are used to estimate the effect of competition on tree growth as a function of neighbour species, size, abundance and distance to target tree (Avery and Burkhart, 2002). Understorey light levels and growing space can be manipulated using silvicultural treatments by varying the cutting intensity, the distribution and the configuration of canopy openings (Beaudet et al., 2011). It is therefore important to understand how partial harvesting treatments influence competition in mixedwood stands in order to better control growth responses of residual trees and maintain desired stand composition and structure.

Sunlight is likely the most limiting resource for white spruce in aspen dominated mixedwood stands (Filipescu and Comeau, 2007; Beaudet et al., 2011). Competition for light is usually referred to as asymmetric since trees in the dominant social class are situated in a favourable position for intercepting the highest proportion of sunlight, thereby supressing trees lower in the canopy (Connolly and Wayne, 1996). Aspen is often considered to have a competitive advantage, at least in the short to medium term, due to its ability to efficiently capture and use resources, resulting in accelerated growth and canopy dominance (Balandier et al., 2006). However, Boivin et al. (2010) found that in young (8-15 year old) mixedwood stands in Quebec, competition was strongest between conspecific neighbours and among the 4 species evaluated in the study, aspen was the weakest competitor. They suggest that the high occurrence (density) of aspen in the stands is related to the species ability to reproduce quickly and root sucker, rather than a strong capacity for competition (Boivin et al., 2010).

Furthermore, according to Man and Lieffers (1997), differences in species traits between white spruce and aspen reduce the effects of competition by differentiating or partitioning resource niches and allow the two species to coexist in the same stands. The foliage of white spruce has lower photosynthetic compensation and saturation points than aspen but is able to fix carbon in diffuse light more efficiently, thus is able to grow and survive under the aspen canopy (Boardman, 1977). Moreover, according to Lieffers and Stadt (1994), while full

sunlight is optimal for maximum diameter growth, white spruce can reach its maximum height growth in 40 to 60% of full sunlight.

Interactions between white spruce and aspen can also be positive. For example, the shade created by the aspen canopy is beneficial in supressing herb and shrub growth which often competes with white spruce seedlings (Lieffers and Stadt, 1994). This is advantageous because white spruce seedlings can take a number of years to attain heights above the shrub layer (Groot, 1999; Filipescu and Comeau, 2007). Aspen is also an important species for nutrient cycling in mixedwoods since it can draw nutrients from deep mineral soil layers and return them to the soil through leaf litter, whereas most conifers generally concentrate their roots in and above the humus layer-mineral soil interface. The process of nutrient recycling by aspen could be particularly critical for juvenile spruce on poor sites (Man and Lieffers, 1999b) and underlines the importance of considering this interaction and other positive relationships of species mixtures when applying partial harvesting treatments that remove the hardwood component.

1.8 Project objectives and hypotheses

Partial harvesting treatments will likely be increasingly incorporated into boreal mixedwood management strategies throughout Canada. Before these relatively new treatments become generalized, it is important to take a precautionary approach to their implementation, one aspect of which is to assess knowledge of tree and stand-level responses from existing silvicultural experiments. The treatments evaluated in this study were initiated in 2001 by the Industrial Chair in Sustainable Forest Management (SFM Chair) at the University of Quebec in Abitibi-Témiscamingue in collaboration with the industrial partner Tembec Industries. The proportion of white spruce basal area in the treated stands was considerably higher than what is generally found in mixed stands in Quebec (and in eastern Canada, generally), which incited Tembec and the SFM Chair to establish the study. The experimental units were established in 2001 and were subjected to partial harvesting in the late summer of 2001 and in the fall of 2002. The treatments consisted of removing four different proportions of canopy aspen (0, 50, 65 and 100% basal area) in order to encourage regeneration and growth of residual conifer stems, primarily white spruce. The purpose of this project is to quantitatively

evaluate and compare the radial and volume growth responses of residual white spruce trees 10 years after the application of the partial harvesting treatments. Moreover, the influence of time since treatment, tree social status (dominant, co-dominant or suppressed), pre-treatment growth rate and neighbourhood competition on post-treatment growth rates will be evaluated. These variables are important for understanding and nuancing the capacity of trees to respond to competition and the increased availability of resources. This project is based on the following hypotheses:

Firstly, the intensity of the partial harvesting treatment will have an effect on the magnitude of growth response. We anticipated that white spruce trees in the 50 and 65% aspen removal treatments would exhibit the highest levels of growth response. These intermediate treatments should transmit adequate levels of sunlight to accelerate white spruce growth rates, while maintaining enough cover to reduce the effects of increased heat, water and wind stress and suppress aspen suckering. Secondly, tree social status will have an effect on the magnitude of growth response. We expected that absolute radial and volume growth would be higher for dominant and co-dominant trees than suppressed trees because of their larger initial size and vigor. However, we further hypothesized that the relative change in resource availability should be greatest for individuals in the supressed social status and therefore, suppressed and co-dominant trees would exhibit greater cumulative relative growth increase than dominants. Finally, the neighbourhood environment surrounding each felled white spruce tree will have an influence on its post-treatment radial and volume growth rate. We anticipated that competition exerted by neighbouring trees would decrease relative to increasing aspen removal and that the competitive effect would be proportional to the number, size and proximity of neighbours.

CHAPTER II

SPRUCING UP EASTERN CANADIAN MIXEDWOODS: DOES WHITE SPRUCE (*PICEA GLAUCA*) RESPOND TO PARTIAL HARVESTING?

2.1 Abstract

Boreal mixedwood stands in eastern Canada are often characterized by a dominant canopy of shade intolerant hardwoods like aspen (*Populus tremuloides* Michx.) with more shade tolerant conifers like white spruce *(Picea glauca* (Moench.)Voss) situated in the mid- to sub-canopy layers. Partial harvesting has been promoted as an alternative treatment to clear-cutting in mixedwood stands. We tested four partial harvesting treatments in mixed aspen - white spruce stands, including a control, consisting of different proportions of aspen removal (0, 50, 65 and 100% basal area (BA)). Ten years after treatments, 72 white spruce stems representing dominant, co-dominant and suppressed social classes were destructively sampled for stem analysis. Using linear mixed effect models, growth was analyzed as a function of treatment intensity, time since treatment, social status, pre-treatment growth rate and neighbourhood competition. Relative to control stands, radial and volume growth responses were detected only in the extreme treatment of 100% aspen BA removal. Compared to control trees, average annual radial and volume increments were, respectively, 23.5% and 7.1% higher for dominant trees, 67.7% and 24.1% higher for co-dominant trees and 115.8% and 65.6% higher for suppressed trees over the 10 years post-treatment. In relative terms, suppressed trees showed the greatest magnitude of cumulative growth increase. Growth response was proportional to pre-treatment growth rate with vigorous, younger trees having highest post-treatment growth rates. Based on Hegyi's competition index, only coniferous neighbours had a negative effect on sampled white spruce growth. For stand types and partial harvesting treatments similar to the ones tested here, we conclude that it is necessary to remove a very high proportion of the shade intolerant hardwoods, and of total stand BA, in order to obtain accelerated white spruce growth rates. The removal of some dominant white spruce trees and thinning of dense conifers may further reduce intraspecific competition and have a positive effect on residual tree growth. These results should contribute to the development of partial harvesting treatments better adapted to the structure and dynamics of boreal mixedwood forests.

2.2 Résumé

Les peuplements mixtes de l'est du Canada sont souvent caractérisés par une dominance d'espèces intolérantes à l'ombre, comme le peuplier faux-tremble (*Populus tremuloides* Michx.), avec une forte composante de conifères plus tolérants, comme l'épinette blanche (*Picea glauca* (Moench.) Voss), situés davantage dans les strates inférieures de la canopée. Dans les peuplements mixtes, les coupes partielles ont été promues comme un traitement sylvicole alternatif à la coupe à blanc. Nous avons testé quatre traitements de coupe partielle dans les peuplements mixtes tremble-épinette blanche, comprenant un témoin, selon quatre intensités de prélèvement de tremble (0, 50, 65 et 100% de la surface terrière (ST)). Dix ans après les traitements, 72 épinettes représentant les classes sociales dominante, co-dominante et supprimée, ont été abattues et des disques récoltés pour fins d'analyses de tiges. À l'aide des modèles mixtes, la croissance a été analysée en fonction des facteurs suivants: intensité du traitement, temps depuis traitement, statut social, taux de croissance avant traitement et compétition des arbres voisins. Par rapport aux peuplements témoins, une réaction positive de croissance a été observée seulement suite au traitement extrême (100% prélèvement du tremble). Comparativement aux arbres témoins, le taux de croissance radiale et en volume ont été supérieures de 23,5% et 7,1% pour les dominants, 67,7% et 24,1% pour les co-dominants et 115,8% et 65,6% pour les arbres supprimés, au cours des dix ans suivant les traitements. En termes de croissance relative, les arbres supprimés ont eu la plus grande hausse de croissance cumulative. Par ailleurs, la réaction de croissance après traitement s'est avérée proportionnelle au taux de croissance avant traitement. En utilisant les indices de compétition de Hegyi, nous avons observé que seuls les voisins conifères ont eu un effet négatif sur la croissance des épinettes échantillonnées. Nos résultats contribueront au développement de systèmes sylvicoles mieux adaptés à la structure et à la dynamique des forêts boréales mixtes.

2.3 Introduction

In much of the south-eastern Canadian boreal forest, mixedwood stands are considered to be in a transitional succession phase (Bergeron, 2000). Mixedwood stands are frequently initiated following large-scale disturbances such as wildfires and, in early stand development, are typically dominated by fast-growing, shade-intolerant hardwoods, such as trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). More shade-tolerant conifer species such as white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*) may seed in immediately after fire from peripheral or patches of intact forest or slowly recruit in the understory in subsequent years following disturbance (Galipeau et al., 1997). Because of differences between aspen and conifer species in terms of regeneration dynamics, shade tolerance and sapling and tree growth, white spruce is often of pre-commercial or of small merchantable size classes when aspen arrives at a stage suitable for commercial harvesting.

Over the last half century, even-aged management has generally been applied across the boreal forest of Quebec, and for reasons of industrial demand, harvesting has largely concentrated in conifer or conifer-dominated mixed stands. One the most evident legacies of this regime, particularly on mesic sites, has been an important increase in intolerant hardwood-dominated mixedwood stands (Laquerre et al., 2009) in which industry is increasingly required to intervene. However, when conifer stems are suitable for harvesting, the aspen have generally surpassed their peak growth period. Therefore, harvesting the two species at the same time results in some loss of stand productivity, since they do not attain their maximum growth rates at the same point in time (MacDonald, 1995).

The removal of the dominant aspen canopy in mature mixedwood stands should, at least temporarily, release residual conifers, in particular the white spruce, from aspen competition. Thus, in this type of treatment, aspen are ideally harvested before succumbing to age-related mortality and white spruce trees are left to occupy the freed-up growing space and exploit the greater availability of light and soil resources. Pre-treatment growth rate has been found to influence post-treatment growth (Thorpe et al., 2007; Bose et al., 2014) and vigorous, small and young trees are generally assumed to have the greatest potential for release. Presumably, the relative change in resource availability should be greatest for individuals in suppressed

social status classes (Bevilacqua et al., 2005; Vincent et al., 2009) but recent studies have demonstrated that larger conifers most often exhibit highest absolute volume growth rates following release treatments (Latham and Tappeiner, 2002; Mäkinen and Isomäki, 2004; Gagné et al., 2012).

One major design challenge is determining the optimum range of canopy opening that will maintain enough cover to suppress competition from shrubs and regenerating aspen, but will also allow an adequate amount of sunlight for the growth release of understory white spruce (Lieffers and Stadt, 1994; Groot, 1999; Comeau et al., 2005). Aspen suckering has been found to increase proportionally with partial harvesting intensity (Prévost and Pothier, 2003; Brais et al., 2004) and due to its fast growth rate, it has the potential to overtop short white spruce trees. In addition, the complete or near-complete removal of canopy trees can negatively impact residual trees by causing physiological shock due to wind, water and heat stress, thus postponing growth responses and/or limiting diameter growth (Youngblood, 1991; Urban et al., 1994).

Though several studies have evaluated partial harvesting in terms of white spruce recruitment and mortality, very few have evaluated the growth responses of residual trees in aspen-white spruce mixedwood stands in eastern Canada. Even fewer have used stem analysis to evaluate tree-level volume responses among different social status classes following partial harvesting treatments. The purpose of this study was to evaluate the effect of partial harvesting treatments on radial and volume growth rates of white spruce trees in mixed stands, over a period of 10 years post-treatment. More specifically, our objectives were to investigate the effect of treatment intensity, tree social status, pre-treatment growth rate and neighbourhood competition on post-treatment annual radial and volume growth of residual white spruce stems. At the beginning of the study, we formulated the following hypotheses: (i) trees in intermediate (50 and 65%) partial harvesting treatments would have superior radial and volume growth rates compared to control stands; (ii) absolute growth rates would be higher for dominant and co-dominant trees than suppressed trees; (iii) cumulative relative growth rates would be higher for suppressed trees than co-dominant and dominant trees; (iv) growth rates would be negatively affected by neighbourhood competition.

2.4 Methods

2.4.1 Study area and site description

The study site is situated in Abitibi-Témiscamingue, Quebec (48°14'32.2"N, 79°17'12.00"W), in the Western balsam fir-white birch (*Betula papyrifera*) biogeoclimatic subdomain (Saucier, 1998). The area is characterized by mesic soils, primarily Grey Luvisols originating from lacustrine clay deposits left by proglacial Lake Ojibway (Vincent and Hardy, 1977). The climate is continental with a daily average temperature of 1.7° C and annual precipitation of 883 mm of which 625 mm falls as rain from April to November (Riviere Kinojevis meterorological station (48°13' N, 78°52' W), Canadian climate normals 1971-2000, (Environment Canada, 2013).

Treated stands were mixed aspen-conifer with mean basal area (BA) of 41 $m^2 \cdot ha^{-1}$ (Table 2.1). Mature aspen dominated the canopy cover with conifers generally distributed through the suppressed to co-dominant canopy layers. Mean white spruce and aspen ages were 71 and 68, respectively. While some old (100 to 120 years) white spruce trees were present in stands, roughly 89% of sampled trees established within 14 years, corresponding to calendar years 1937 to 1950. Aspen establishment generally occurred throughout the same time period, but recruitment was more gradual. Basal area distribution of control stands at time of treatments was 75% aspen (includes balsam poplar), 20% white spruce, 3% balsam fir, 1% black spruce (*Picea mariana*) and 1% white birch.

2.4.2 Experimental design and treatments

Experimental units were laid out based on prism inventories done prior to treatments. Partial harvesting prescriptions were applied to the experimental units in the late summer of 2001 and the fall of 2002. Trees were manually harvested, limbed and cut to length on site and hauled to roadside using narrow-tracked skidders and forwarders in order to minimize damage to residual trees during harvesting operations. Treatments consisted of removing various proportions of aspen in order to encourage the growth of residual conifer stems,

primarily white spruce, and promote conifer recruitment. Treatments consisted of a no-harvest control, (0% BA removal), two intermediate treatments that removed 50 and 65% of aspen BA and an extreme treatment of 100% aspen BA removal (Table 2.1). Each treatment was repeated three times for a total of twelve experimental units. Immediately following treatments a total of thirty, 400 m^2 circular permanent sample plots (PSPs, radius=11.28 m) were established (9 in each of the two intermediate treatments and 6 in the control and total treatments). Stems greater than 5 cm in diameter at breast height (DBH, 1.3 m) were tagged, measured and identified to species. PSPs established in year 0 were re-measured at 5 and 10 years post-treatment.

2.4.3 Sampling

In 2012, all experimental units had attained the 10 year post-treatment period. In the summer of 2012, destructive sampling was conducted for tree growth analyses. This consisted of harvesting a total of 72 residual white spruce trees from controls and partially cut stands. Trees selected for felling were live and vigorous with little to no external evidence of disease. Two trees from each of three different social status classes (dominant, co-dominant and suppressed), were selected from each experimental unit. While recognizing that social status is a classification of vertical crown position of a tree relative to all other tree crowns in a stand, we used tree diameter distribution as a proxy for height distribution in each experimental unit. Also, given that aspen generally occupied the dominant social class with only a minor component of spruce, assignment of social status to individuals was based exclusively on the relative size among the white spruce trees, rather than the true interspecific social status of all trees within the stand. Stem size distribution was calculated for each experimental unit based on white spruce trees in the PSPs and the following classification was used to select individual trees to be destructively sampled from each social status class: dominant trees: diameter size class $\geq$ 2 standard deviations (SD) of mean DBH; co-dominant trees: size class of $\geq$ 1 SD of mean DBH; suppressed trees $\leq$ the mean DBH. Following felling, crown length was measured and live crown ratio for each tree was determined. Branch length was measured at each disk height and crown width was taken as the sum of the two longest branches from opposite sides of the crown (Table 2.2).

Cross sectional disks were sampled from 11 positions along the length of the stem of each tree. The first disk was taken at 0.3 m stump height and the second from 1.3 m, breast height (BH). The remaining 9 disks were sectioned from equally spaced positions relative to length of the stem from BH to the top of the tree (Chhin et al., 2010). All disks were marked to identify the tree number and to specify the height at which each was collected. In order to determine minimum age of canopy aspen, stems ≥20 cm DBH situated closest to each collected white spruce stem were cored at 1 m in control, 50% and 65% BA removal experimental units.

2.4.4 Neighbourhood competition assessment

At the time of felling, the neighbourhood environment of each collected (target) white spruce tree was assessed in circular plots within a 10 m radius of each felled tree (Hartmann et al., 2009). All standing trees (≥10 cm DBH) within the neighbourhood area were identified to species level and measured for DBH and distance to the felled white spruce tree (Canham et al., 2004; Hartmann et al., 2009). Neighbourhood competition was assessed to quantitatively evaluate the influence of competition on the radial and volume growth rates of target trees. Hegyi's (1974) neighbourhood competition index (HCI) was calculated for all neighbour trees within the 10 m radius of each sampled white spruce tree. Distance-independent HCIs were calculated as a function of the white spruce and neighbour tree DBH's. Distance-dependent HCIs incorporated the distance between each neighbour tree and the target white spruce tree in the calculation. Hegyi's HCI was then adapted based on additional conditions including: neighbour tree type (broadleaf species consisting of: aspen, balsam poplar, white birch or coniferous species consisting of: white spruce, black spruce, balsam fir, jack pine) and distance to the sampled white spruce stem (≤10 m, ≤ 8 m, ≤6 m, ≤ 5 m, 5-10 m). In total, 30 variations of the HCI were computed (Annex B, Table B.1).

Distance-independent equation is given as,

$$\mathrm{HCI} = \sum_{i=1}^{n} \frac{\mathrm{dbh}_i}{(\mathrm{dbh}_t)}$$

Distance-dependent equation is given as,

$$HCI = \sum_{i=1}^{n} \frac{dbh_i}{(dbh_t)(distance_{it})}$$

where, dbh_i is neighbour tree diameter at breast height (cm); dbh_t is target tree diameter at breast height (cm); $distance_{it}$ is the horizontal distance (m) between neighbour (i) and target tree (t).

2.4.5 Disk preparation and measurements

All white spruce cross sectional disks and aspen radial cores were dried and sanded with progressively finer grit sand paper in order to clearly discern the annual growth rings. Samples were analyzed in the laboratory using dendroecological procedures to count and measure annual radial growth increments. Disks were visually cross dated using a microscope in order to identify any false or missing rings, and were scanned for image analysis. Annual ring widths were measured along 3 radii per disk using WinDendro (Regent Instruments Canada Inc., 2009). The ring width data obtained from WinDendro was further analyzed using WinStem (Regent Instruments Canada Inc., 2004) which computed average annual radial growth increments ($mm \cdot yr^{-1}$) for each disk and was used to reconstruct annual volume increments ($dm^3 \cdot yr^1$). Radial growth rates at 1.3 m and volume growth rates for the entire stem, over the last 15 years of growth were used for statistical analyses. Pre-treatment growth rate was taken as the average annual growth rate in the 5 years prior to treatment while post-treatment growth rates were the annual increments for each year in the 10 year post-treatment period.

Because radial growth rates generally decrease following a period of rapid growth in the juvenile stage (Annex A, Fig. A.7), cambial age at 1.3 m was measured and used to account for age effects in statistical analyses. To determine general age of white spruce trees in the stand, minimum tree age of white spruce was taken from cambial age at 0.3 m. The aspen cores were aged under the microscope to determine the minimum age of aspen in the stand. Relative cumulative growth (%) was determined for each social status-treatment combination, using annual cumulative radial and volume growth for each year in the 10 years post-treatment. This information was not analyzed statistically, but was used to determine which social status showed the greatest magnitude in growth response over the 10 years.

Table 2.1 Characteristics of the 12 experimental units.

Treatment intensity and year of treatment	Replicate	Initial BA ($m^2 \cdot ha^{-1}$)[a]	BA post-treatment ($m^2 \cdot ha^{-1}$)	BA 5 years post-treatment ($m^2 \cdot ha^{-1}$)	BA 10 years post-treatment ($m^2 \cdot ha^{-1}$)	% stand removed	% aspen removed	Experimental Unit Area (ha)
Control								
N/A	1	39.89	42.65	47.2	49.4	0	0	1.2
N/A	2	38.56	40.32	37.5	39.4	0	0	0.8
N/A	3	39.14	46.91	49.2	54.8	0	0	1.0
50% Aspen BA removal								
2002	1	37.50	25.69	29.7	31.1	31	53	2.8
2002	2	37.88	25.92	29.8	34.0	32	52	3.8
2002	3	38.79	22.32	28.3	33.6	42	52	3.4
65% Aspen BA removal								
2002	1	44.19	26.20	27.3	28.8	41	64	2.4
2002	2	34.40	16.82	19.5	22.3	51	74	3.8
2001	3	41.30	23.49	22.1	26.4	43	61	3.5
100% Aspen BA removal								
2002	1	51.08	14.12	8.0	11.4	72	93	2.0
2002	2	31.65	11.44	14.1	18.1	64	100	2.0
2001	3	58.04	10.03	7.3	12.4	83	99	3.5

[a] Initial BA values were derived from prism inventories prior to treatments, whereas BA post-treatment values were derived from PSPs established immediately following treatments and were re-measured at years 5 and 10 post-treatment.

Table 2.2 Characteristics of white spruce trees destructively sampled in 2012 from boreal mixedwood stands subjected to partial harvesting in 2001-2002.

Treatment intensity and social status	Mean DBH (cm)	DBH range (cm)	Mean height (m)	Height range (m)	Mean crown length (m)	Crown length range (m)	Mean live crown ratio	Mean crown width (m)	Crown width range (m)
Control									
dominant	34.3	29.8-38.1	23.5	19.4-26.9	16.3	10.5-19.3	0.69	5.9	5.3-6.7
co-dominant	18.1	16.5-19.9	15.6	13.0-19.8	10.5	9.7-11.7	0.69	4.6	3.3-5.6
suppressed	11.5	9.0-13.8	10.5	7.8-12.3	5.6	3.4-7.5	0.53	4.0	3.0-5.1
50% Aspen BA removal									
dominant	30.1	25.1-40.3	21.7	18.4-24.6	15.5	12.0-20.3	0.71	5.6	4.1-7.2
co-dominant	19.3	13.6-24.1	14.8	11.3-20.4	10.1	6.6-14.2	0.67	4.9	3.5-5.8
suppressed	12.4	9.7-14.3	10.9	10.4-11.3	6.4	5.3-8.6	0.59	3.6	3.1-4.4
65% Aspen BA removal									
dominant	38.2	28.2-49.2	25.4	22.3-30.2	20.9	17.2-23.8	0.83	6.9	5.1-8.6
co-dominant	19.8	18.3-20.9	16.7	13.4-19.9	10.5	7.3-13.9	0.64	4.2	2.9-5.8
suppressed	13.0	11.2-13.8	10.6	9.7-12.3	6.7	3.1-10.1	0.63	4.0	2.6-4.7
100% Aspen BA removal									
dominant	36.4	28.4-54.0	21.7	18.4-26.7	16.8	13.2-20.1	0.78	7.6	3.9-9.2
co-dominant	19.5	17.8-20.9	13.7	12.4-16.0	8.5	5.7-10.4	0.63	4.8	3.9-5.7
suppressed	12.7	10.3-15.5	9.5	6.8-12.4	5.6	3.2-8.5	0.61	3.9	2.2-4.8

2.4.6 Statistical analyses

2.4.6.1 Model selection and Linear mixed effect models

Statistical analyses were conducted using the nlme package (Pinheiro et al., 2013) in R (R Core Development Team, 2012). Linear mixed effect models were used to account for the non-independence of data since white spruce trees were nested within experimental units and repeated measurements (annual growth rates) were taken from each individual tree. Model selection based on Akaike's information criteria corrected for small sample sizes (AICc) was accomplished using the AICcmodavg package (Mazerolle, 2013) in R. The model with the lowest AICc value was considered to be the most parsimonious. For each analysis, growth predictions, model average estimates and unconditional 95% confidence intervals were based on the entire set of candidate models, using the AICcmodavg package (Mazerolle, 2013).

2.4.6.2 Treatment intensity, social status, pre-treatment growth rate, time and cambial age

Fifteen competing models (Annex B, Table B.2), including a null model, were tested to determine the effects of partial harvesting treatments, tree social status and pre-treatment growth rates on post-treatment radial and volume growth rates in the 10 years following treatments. Treatment intensity and social status were treated as categorical variables while pre-treatment growth rate and time were treated as continuous variables. Seven of the models included the squared value of time ($time^2$), to account for quadratic effects while the remaining models (excluding the null model) accounted for linear effects of time. Cambial age at 1.3 m was also included in all models (excluding the null model), when the response variable was radial growth rate. Specific interactions were included in the models to determine how growth changed over time and whether growth of the three social statuses was similar across all treatment intensities. The above mentioned variables were considered as fixed factors in the mixed effect models. Tree number and experimental unit were considered as random effects. Transformations were applied to response variables to ensure model assumptions were met (normality and homoscedasticity of residuals). A square root

transformation was applied to radial growth rate and a log transformation was applied to volume growth rate.

2.4.6.3 Selection of most parsimonious Hegyi Competition Index (HCI)

The same model selection approach was used to determine which variant of the 30 HCIs best explained radial and volume growth rates of collected white spruce trees. Each HCI was considered as a separate model and a null model was included in the analyses (Annex B, Table B.1). Since the competitive effect of neighbours changes through time, the HCIs were assumed to be representative of competition only in the last few years of growth before stem collection. Therefore, average growth rates in the last 3 years (years 8, 9, 10 post-treatment) were analyzed as a function of HCI. Both average radial and volume growth rates in the last 3 years were log transformed to meet model assumptions. For these analyses, HCI was considered as the fixed effect and experimental unit was considered as the random effect. The most parsimonious models, or best HCI explaining radial growth and best HCI explaining volume growth, were included in the subsequent analyses.

2.4.6.4 Treatment intensity, social status, pre-treatment growth rate, HCI and cambial age

After selecting the best HCIs explaining neighbourhood competition, nine additional models (Annex B, Table B.3) were tested using the same model selection approach, to determine the effects of partial harvesting treatments, social status, pre-treatment growth rate and HCI on average radial and volume growth rates in the last 3 years (years 8, 9, 10 post-treatment). Cambial age at 1.3 m was also included in all models (excluding the null model), when the response variable was radial growth rate. Specific interactions were included in the models. These variables were considered as the fixed factors, and experimental unit was considered as the random factor. Datasets were not transformed prior to analyses since they conformed to model assumptions.

2.5 Results

2.5.1 Treatment intensity, social status, pre-treatment growth rate, time and cambial age

When considering both annual radial and volume growth rates as response variables, the most parsimonious model was that which included the additive effects of treatment intensity, social status, time, time^2, pre-treatment growth rate and cambial age (for radial growth) as well as the interactions between treatment and time and treatment and time^2 (Table 2.3).

For radial growth, the top ranking model was clearly the most probable (AICc Wt. 1.0, Table 2.3). In terms of volume growth, the most likely model (AICc Wt. 0.68) was 2.13 times more parsimonious than the second ranking model (Table 2.3). The second ranking model included the same variables as the top model but excluded the quadratic effect of time (time^2).

Annual radial and volume growth rates for white spruce trees in the two intermediate partial harvesting treatments (50 and 65%) were similar to control stands. The extreme partial harvesting treatment of 100% aspen BA removal did, however, have a positive effect on both radial and volume growth rates of residual white spruce trees in the 10 years following treatment (Table 2.4). Radial and volume growth rates were superior to control stands, and this effect was evident across all three social statuses.

The treatment effect was immediate with growth rates increasing within the first two years following treatment. Radial growth followed a negative quadratic form with peak growth rates occurring at approximately 6 years post-treatment, then gradually decreasing from 6 to 10 years following treatment (Fig. 2.1). This pattern was apparent for all three social statuses. Volume growth followed a similar negative quadratic form, though growth rate continued to increase throughout the 10 year period (Fig. 2.2).

Table 2.3 Results of model selection for mixed linear effects models based on Akaike's Information Criterion corrected for small sample size (AICc). Annual radial growth rate ($mm \cdot year^{-1}$) at 1.3 m and annual volume growth rate along the stem ($dm^3 \cdot year^{-1}$) for residual white spruce trees 10 years following partial harvesting treatments was analyzed as a function of treatment intensity[a] (intensity), time[b] (time), social status[c] (ss), pre-treatment growth rate[d] (pre-treat) and cambial age[e] (age). Interactions between variables are specified with a colon. Only the most probable models are shown for brevity.

Model	K	AICc	ΔAICc	AICc Wt.	R^2
Radial growth at 1.3 m ($mm \cdot year^{-1}$)					
age + intensity + ss + time + $time^2$ +pre-treat + intensity:time + intensity:$time^2$	19	-296.63	0.00	1	0.83
Volume growth along the stem ($dm^3 \cdot year^{-1}$)					
intensity + ss + time + $time^2$ + pre-treat + intensity:time + intensity:$time^2$	18	523.44	0.00	0.68	0.94
intensity + ss + time + pre-treatment growth rate + intensity:time	14	524.95	1.52	0.32	0.94

K: number of parameters

AICc: Akaike's Information Criterion corrected for small sample size

ΔAICc: AICc relative to most parsimonious model

AICc Wt.: model weight

[a] Treatment intensity: control, 50%, 65%, 100% aspen basal area removal

[b] Time and $time^2$ were tested to determine linear and quadratic effects

[c] Intraspecific social status of residual white spruce trees: suppressed, co-dominant, dominant

[d] The average annual radial growth rate 5 years prior to treatment

[e] Cambial age taken at 1.3 m (used to analyze radial growth only)

Table 2.4 Model averaged estimates and their 95% confidence interval (CI) based on model selection for mixed linear effects models. Only parameter estimates for terms which exclude 0 in the confidence interval are presented. Response variables are annual radial growth rate at 1.3 m ($mm \cdot year^{-1}$) and annual volume growth rate along the stem ($dm^3 \cdot year^{-1}$).

Term	Estimate	Lower CI	Upper CI
Radial growth at 1.3 m ($mm \cdot year^{-1}$)			
time	0.0275	0.0048	0.0502
$time^2$	-0.0026	-0.0043	-8e-04
pre-treatment growth rate	0.3617	0.2652	0.4583
intensity 4 (100% aspen BA removal)	0.2966	0.1311	0.4620
intensity 4: time	0.1511	0.0976	0.2047
intensity 4: $time^2$	-0.0115	-0.0162	-0.0067
Volume growth along the stem ($dm^3 \cdot year^{-1}$)			
time	0.0217	0.0024	0.041
ss 2 (co-dominant)	0.9391	0.6876	1.1907
ss 3 (dominant)	1.3049	0.8358	1.774
pre-treatment growth rate	0.0489	0.0300	0.0679
intensity 4 (100% aspen BA removal)	0.3814	0.0992	0.6636
intensity 4: time	0.1414	0.0050	0.2778
intensity 4: $time^2$	-0.0111	-0.0194	-0.0029

Since the treatment effect was independent of tree social status, dominant, co-dominant and suppressed trees reacted similarly to the aspen removal (Fig. 2.1 and 2.2). While radial growth rates were similar for all three social classes, volume growth rates were superior for dominant and co-dominant trees compared to suppressed trees (Table 2.4). Suppressed trees however, exhibited the highest relative increase in cumulative radial and volume growth (Fig. 2.1 and 2.2). This was apparent in all treatments including the control, but the greatest increase was observed in the 100% aspen removal treatment. Pre-treatment growth rate affected both radial and volume growth (Table 2.4); trees with superior average growth rates in the five years prior to treatment continued to have superior growth rates in the post-treatment period. For radial growth, this variable was a stronger predictor of post-treatment growth rate than tree social status (Table 2.4).

2.5.2 Neighbourhood competition

The highest ranking HCI for radial growth (AICc Wt. 0.79) was a distance independent model that accounted for competition with coniferous neighbours only within a 5 m radius (Table 2.5). In terms of volume growth, neighbourhood competition was best explained (AICc Wt. 0.68) by a distance dependent HCI, also accounting for competition with coniferous neighbours only, but within a 10 m radius of the sampled white spruce trees (Table 2.5). These respective top ranking HCIs were used in subsequent analyses to determine the effect of coniferous neighbourhood competition on the radial and volume growth rates of the white spruce trees.

Table 2.5 Results of model selection for mixed linear effects models based on Akaike's Information Criterion corrected for small sample size (AICc). Average annual radial growth rate ($mm \cdot year^{-1}$) at 1.3 m and average annual volume growth rate along the stem ($dm^3 \cdot year^{-1}$) of residual white spruce trees in the last 3 years of growth was analyzed as a function of the 30 variations of Hegyi's competition index (HCI). Only the most probable models are shown for brevity.

Model	K	AICc	ΔAICc	AICc Wt.	R^2
Radial growth at 1.3 m ($mm \cdot year^{-1}$)					
HCI13	4	111.49	0.00	0.79	0.56
HCI22	4	115.64	4.15	0.10	0.53
Volume growth along the stem ($dm^3 \cdot year^{-1}$)					
HCI22	4	140.12	0.00	0.68	0.72
HCI13	4	141.72	1.59	0.31	0.71

2.5.3 Treatment intensity, social status, pre-treatment growth rate, HCI and cambial age

Average annual radial growth in the last 3 years following partial harvesting treatments was best explained by the model which accounted for the additive effects of treatment intensity, HCI, pre-treatment growth rate and cambial age. This top model (AICc Wt. 0.89) was 9.9 times more parsimonious than the second ranking model (AICc Wt. 0.09, ΔAICc 4.58, Table 2.6). This same model, excluding cambial age, was also the most parsimonious in terms of volume growth (AICc Wt. 0.75), although the second ranking model accounting for additive effects of HCI and pre-treatment growth rate was also highly probable (ΔAICc 2.94, Table 2.6).

Radial and volume growth rates differed depending on partial harvesting intensity, with white spruce trees in the 100% aspen BA removal treatment continuing to show improved growth rates over the control in years 8, 9 and 10 following treatment (Table 2.7). No differences were found between the two intermediate treatments (50 and 65%) and control stands.

The treatment effect was independent of tree social status; in fact, models that included social status ranked relatively low. Average pre-treatment growth rate was an important factor affecting growth in that trees with high pre-treatment growth rates showed higher growth rates 7 to 10 years post-treatment (Table 2.7). Furthermore, as cambial age increased, radial growth rates decreased (Table 2.7). Mean pre-treatment radial growth rate was higher for dominant trees compared to co-dominant and suppressed, but some dominant trees had low pre-treatment growth rates, equivalent to the mean pre-treatment values of suppressed trees (0.75 $mm \cdot year^{-1}$). When considering the mean increment over the 10 year post-treatment period, the smaller, suppressed trees had superior radial growth rates when the pre-treatment radial growth rate was low (0 to 1.9$mm \cdot year^{-1}$). No suppressed trees had high pre-treatment growth rates (2.0 to 3.8$mm \cdot year^{-1}$), but mean increment over the 10 year post-treatment period was higher for co-dominant and dominant trees with pre-treatment growth rates in this range. Co-dominant and dominant trees younger than median age of 52 at time of treatment all had high pre-treatment growth rates (0.95 to 3.8 $mm \cdot year^{-1}$) whereas trees older than 52 generally had low pre-treatment growth rates (0 to 2.84 $mm \cdot year^{-1}$) and older suppressed trees had very low pre-treatment growth rates (0 to 0.95$mm \cdot year^{-1}$). Of the older aged trees, co-dominants had higher mean increments over the 10 year post-treatment period, despite having low pre-treatment values.

Neighbourhood competition as explained by the HCIs, negatively affected both radial and volume growth rates (Table 2.7). The most parsimonious neighbourhood competition indices were those that accounted for competition with coniferous species only (Table 2.5). Radial growth was negatively influenced by conifer trees located anywhere within a 5 m radius to the white spruce trees regardless of actual proximity, whereas white spruce volume growth was negatively affected by conifer trees within a 10 m radius, with both DBH and proximity of neighbour trees influencing the competitive effect.

Table 2.6 Results of model selection for mixed linear effects models based on Akaike's Information Criterion corrected for small sample size (AICc). Average annual radial growth rate ($mm \cdot year^{-1}$) at 1.3 m and average annual volume growth rate along the stem ($dm^3 \cdot year^{-1}$) of residual white spruce trees in the last 3 years following partial harvesting treatments was analyzed as a function of treatment intensity[a] (intensity), social status[b] (ss), neighbourhood competition[c] (HCI), pre-treatment growth rate[d] (pre-treat) and cambial age[e] (age). Interactions between variables are specified with a colon. Only the most probable models are shown for brevity.

Model	K	AICc	ΔAICc	AICc Wt.	R^2
Radial growth at 1.3 m ($mm \cdot year^{-1}$)					
age +intensity + HCI + pre-treat	9	138.97	0.00	0.89	0.63
age +intensity + HCI + pre-treat + intensity:HCI	12	143.55	4.58	0.09	0.65
Volume growth along the stem ($dm^3 \cdot year^{-1}$)					
intensity + HCI + pre-treat	8	397.66	0.00	0.75	0.89
HCI + pre-treat	5	400.60	2.94	0.17	0.89

K: number of parameters

AICc: Akaike's Information Criterion corrected for small sample size

ΔAICc: AICc relative to most parsimonious model

AICc Wt.: model weight

[a] Treatment intensity: control, 50%, 65%, 100% aspen basal area removal

[b] Intraspecific social status of residual white spruce trees: suppressed, co-dominant, dominant

[c] Neighbourhood competition as determined using the most parsimonious competition index

[d] The average annual radial growth rate 5 years prior to treatment

[e] Cambial age taken at 1.3 m (used to analyze radial growth only)

Table 2.7 Model averaged estimates and their 95% confidence interval (CI) based on model selection for mixed linear effects models. Only parameter estimates for terms which exclude 0 in the confidence interval are presented. Response variables are average annual radial growth rate ($mm \cdot year^{-1}$) at 1.3m and average annual volume growth rate along the stem ($dm^3 \cdot year^{-1}$) of residual white spruce trees in the last 3 years following partial cutting treatments.

Term	Estimate	Lower CI	Upper CI
Radial growth at 1.3m ($mm \cdot year^{-1}$)			
pre-treatment growth rate	0.3554	0.1094	0.6014
HCI13	-0.0957	-0.1457	-0.0458
cambial age	-0.0207	-0.0329	-0.0086
intensity 4 (100% aspen BA removal)	0.8050	0.4443	1.1657
Volume growth along the stem ($dm^3 \cdot year^{-1}$)			
pre-treatment growth rate	0.7792	0.6765	0.8818
HCI22	-0.6447	-1.0369	-0.2525
intensity 4 (100% aspen BA removal)	3.4356	1.1755	5.6956

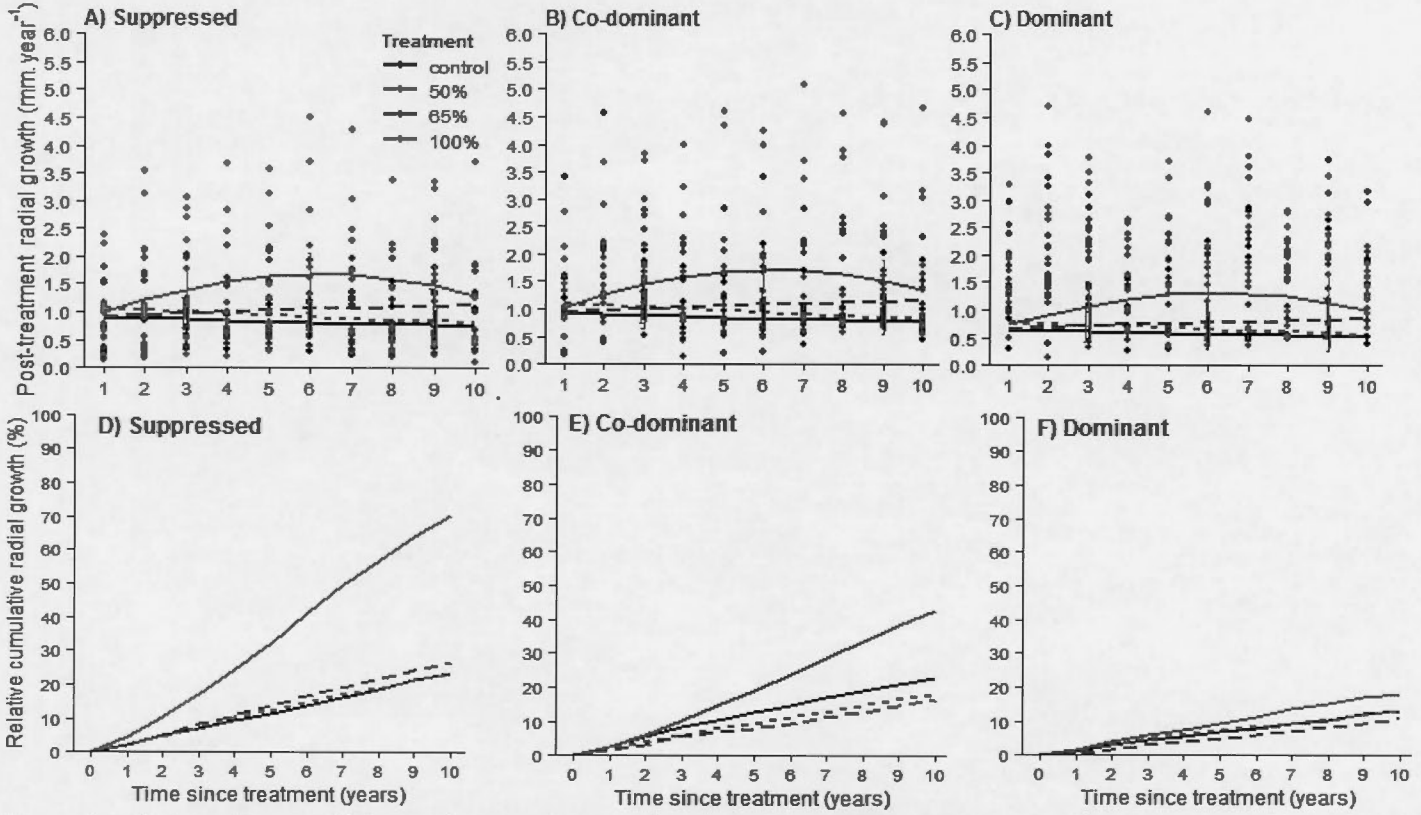

Figure 2.1 Post-treatment radial growth presented as a function of time since treatment for (A) suppressed, (B) co-dominant and (C) dominant trees. Lines represent predicted values. Since pre-treatment growth rates were highly variable amongst the social statues, there was no common value across all three classes that could be used to make predictions. Therefore a value of 0.75 representing the minimum pre-treatment growth rate of dominant trees was used. A value of 50.75 representing mean cambial age of all trees was used to make predictions. Points represent observed values. Relative cumulative radial growth (%) of residual white spruce trees by social status for (D) suppressed, (E) co-dominant and (F) dominant trees.

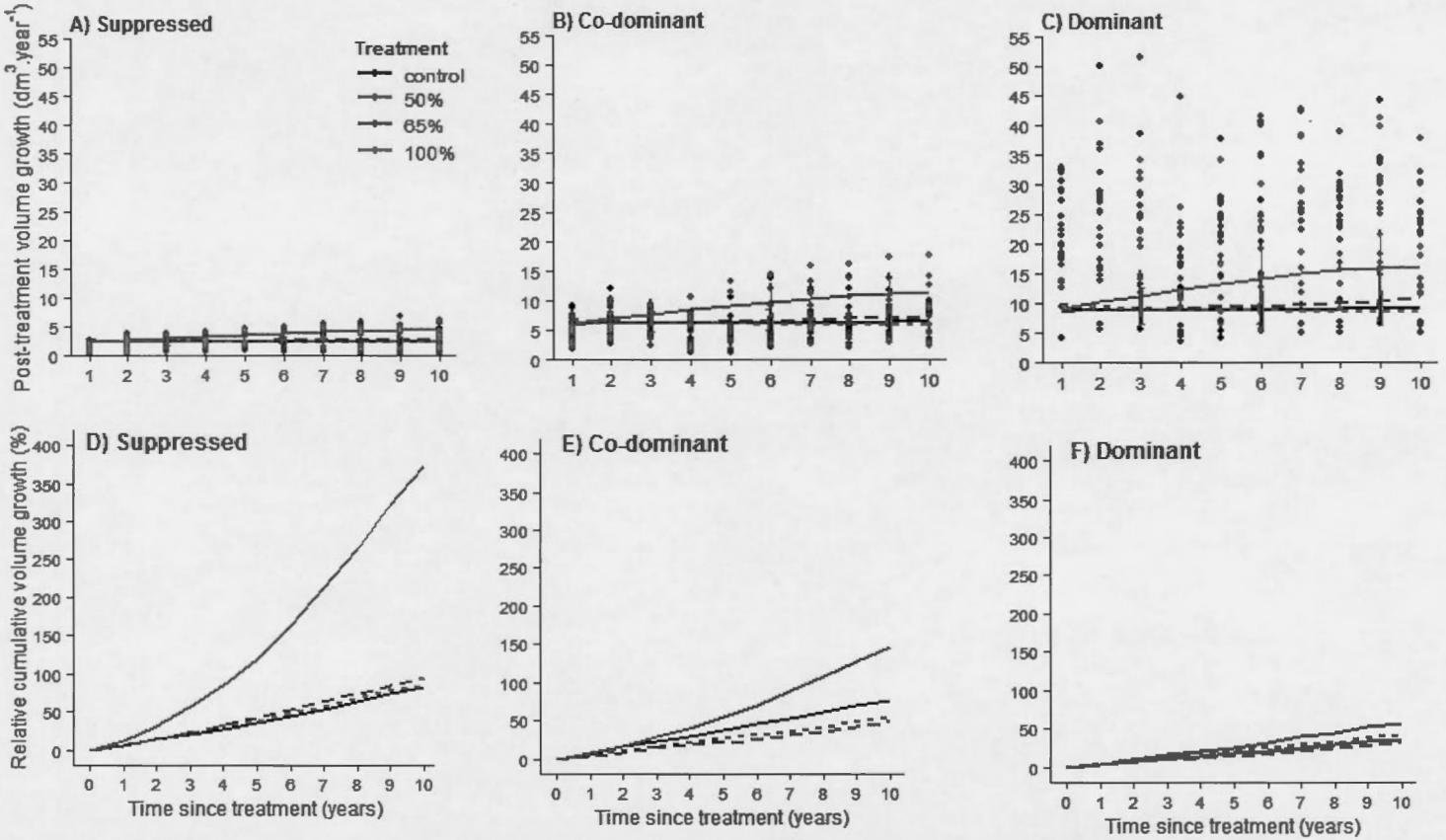

Figure 2.2 Post-treatment volume growth presented as a function of time since treatment for (A) suppressed, (B) co-dominant and (C) dominant trees. Lines represent predicted values. A value of 9.23 representing mean pre-treatment growth rate of all trees was used to make predictions. Points represent observed values. Relative cumulative volume growth (%) of residual white spruce trees by social status for (D) suppressed, (E) co-dominant and (F) dominant trees.

2.6 Discussion

Partial harvesting treatments, where dominant and co-dominant aspen trees were removed, were successful in releasing residual merchantable-sized (≥10 cm DBH) white spruce trees. Based on the results of this experiment, it was necessary to remove 100% of dominant and co-dominant shade intolerant broadleaved trees to significantly accelerate radial and volume growth rates of white spruce. Growth responses were best explained by treatment intensity, time since treatment, tree social status, pre-treatment growth rate and neighbourhood competition.

2.6.1 Treatment intensity

We hypothesized that intermediate treatments (50 and 65% aspen BA removal) would induce the greatest growth response in the residual white spruce trees. It was expected that moderate removal of canopy aspen would increase incident light levels enough to produce a positive growth response in white spruce trees, while not altering growing conditions to a level that might create an effect of growth shock (Urban et al., 1994; Vincent et al., 2009) or induce high levels of aspen suckering (Prévost and Pothier 2003; Brais et al., 2004).

White spruce is considered a moderately shade-tolerant species and although physiological traits, such as low photosynthetic compensation and saturation points, allow the species to fix carbon more efficiently than aspen in low light, competition for light is often regarded as one of the most limiting factors affecting white spruce growth (Lieffers and Stadt, 1994; Lieffers et al., 2002; Comeau et al., 2005). According to Coates and Burton (1999), photosynthetic saturation occurs between 40 and 60% of full sunlight and white spruce seedlings require 40% full sunlight to attain maximum height growth (Lieffers and Stadt, 1994). While light requirements may change through tree development (Claveau et al., 2002), based on these values, an optimal cutting intensity was expected to be between 45 to 65% stand BA removal (Prévost and Pothier, 2003; Beaudet et al., 2011). The two intermediate treatments translated to relatively low levels of total stand BA removal. In the 50 and 65% treatments total BA removal ranged from 31-42% and 41-51%, respectively. Even the more intense 65%

treatment was at the lower end of the spectrum (Table 2.1). Although light transmittance was not measured in the present study, it is clear that the intermediate harvesting intensities did not sufficiently improve light availability, as white spruce growth continued to be inhibited by residual aspen cover. If it is presumed that residual trees are more strongly influenced by the environment created following treatment, rather than what is removed during harvesting, then it is not surprising that trees in the 65% treatment did not exhibit enhanced growth rates over the 50% aspen BA removal treatment. Ultimately, due to differences in initial stand BA, both post-treatment residual BA and the proportion of broadleaf and conifer species were relatively similar in the two intermediate treatments (Table 2.1).

In contrast, white spruce trees displayed significant increases in radial and volume growth rates in the extreme partial cutting treatment where 100% aspen BA harvesting translated into 64-83% total stand BA removal. Compared to control trees, average annual radial and volume increments were, respectively, 23.5% and 7.1% higher for dominant trees, 67.7% and 24.1% higher for co-dominant trees and 115.8% and 65.6% higher for suppressed trees over the 10 years post-treatment. These findings are consistent with similar studies for white spruce release following partial harvesting and thinning treatments (Man and Greenway, 2004; Gagné et al., 2012).

In a 174 year old nearly pure (90% overstory trees), white spruce stand in Alaska, Youngblood (1991) determined that compard to pre-treatment growth rates, radial growth of white spruce trees increased an average of 27% per year, over a period of 8 years following a moderate thinning of 66% total stand BA. The thinning treatment corresponded to the seed cut of a regular shelterwood system, designed to encourage white spruce regeneration by leaving 100 co-dominant and dominant white spruce seed trees in the stand. Residual white spruce trees exhibited a net mean increase in diameter growth of 164%, with peak growth rate occurring 8 years post-treatment.

Fifty years after light thinning (44% stand BA removal) and moderate thinning (60% stand BA removal) in mixedwood stands in Manitoba, Yang (1989) reported that white spruce trees in mixedwood stands in Manitoba responded positively to partial removal of aspen overstory that consisted of two thinning intensities, a light thinning of 44% stand BA removal and a

moderate thinning of 60% stand BA removal. Compared to control trees, diameter and volume increments showed 28% and 81% and 50% and 260% improvement for light and moderate thinning, respectively. In the same study, but for sites situated in Saskatchewan, Yang (1989) found that when subjected to complete aspen removal, white spruce diameter increment improved 50-177% while volume increment improved 24-304% compared to control trees over a period of 35 years.

Similarly, in stands ranging from 5 to 65 years in Alberta, Yang (1991) observed improved growth rates of white spruce when direct aspen neighbours within a circular area two times the crown radius were removed and herbicide treatments applied to aspen stumps. Residual trees showed 41% improvement in diameter growth and 82% increase in volume growth compared to control trees over a post-treatment period of 35 years.

More recently in Alberta, 77 year old aspen-white spruce mixedwood stands were subjected to two pass strip cutting. Its effect on pre-commercial, understory white spruce growth was evaluated by Grover et al., (2014). In this system, the feller buncher was restricted to 8 m wide corridors and extracted broadleaf trees, particularly the dominant aspen, up to 8 m on either side of the trail. A 24 m wide unharvested strip was maintained between the cut strips to protect residual trees from windthrow. Throughout the 10 year monitoring period, Grover et al. (2014) found that annual diameter and volume growth increments were, respectively, 152% and 83% higher for released white spruce compared to controls.

2.6.2 Time

Growth responses to the 100% partial harvesting prescription were apparent within the first two years following treatment. The lack of thinning shock and absence of an extended time lag in growth response was somewhat surprising since these effects have been observed for white spruce (Youngblood, 1991; Urban et al., 1994) and other conifer species following partial harvesting (Kneeshaw et al., 2002; Latham and Tappeiner, 2002; Bebber et al., 2004; Thorpe et al., 2007; Vincent et al., 2009). Environmental conditions created following harvesting apparently did not induce enough physiological stress to hinder an immediate positive growth response to the treatment. Compared to control trees, radial growth was more

responsive than volume over the 10 years, but the effect was not sustained through time. Radial growth rate peaked approximately 6 years following treatment, then gradually decreased from 6 to 10 years post-treatment. Alternatively, volume growth was essentially linear, with growth rates continuing to increase throughout the 10 years. Surprisingly, for trees in the 100% treatment, cumulative volume growth over the post-treatment period was much higher than cumulative radial growth with suppressed, co-dominant and dominant trees having 373, 147 and 57% increases, respectively. This is compared to more modest increases of 84, 77 and 34% for the respective social classes in control stands.

2.6.3 Social status, pre-treatment growth rate and cambial age

Using diameter distribution as a proxy to height distribution was effective in partitioning dominant, co-dominant and suppressed social classes of white spruce trees in each experimental unit (Annex A, Fig. A.4, DBH vs height, $R^2 = 0.84$). Social status at the time of treatment was maintained throughout the post-treatment period; that is, an individual's social status did not change as a result of treatment (Annex A, Fig. A.5, DBH year 0 vs DBH year 10, $R^2 = 0.96$).

We hypothesized that social status would have an effect on the magnitude of radial and volume growth responses of white spruce. Overall, radial growth was superior in the 100% aspen removal treatment compared to controls, however, no differences in absolute growth rates were found between the three social classes. Cambial age at the time of treatment has a direct influence on increment growth potential and affected post-treatment radial growth. Young cambium is more effective than older cambium in producing new wood cells and thicker annual rings (Vaganov et al., 2006). Radial (and diameter) growth rates decrease after maximum annual increment has been reached, so old trees have slower radial growth rates than younger trees of the same size (Jogiste, 2000). However, there is also a possible geometric explanation for lower radial growth in dominant stems: as tree diameter increases, annual rings are added to an increasingly larger circumference, so annual BA increment may remain constant or increase despite decreases in radial growth (A. Achim, pers. Comm.).

As expected, absolute volume growth was directly related to social status, with highest increment occurring in dominant trees, followed by co-dominants and finally suppressed. This has been observed for white and black spruce grown in thinned plantations (Gagné et al., 2012) and natural stands in Quebec (Vincent et al., 2009) and for thinned stands of Norway spruce in Finland (Mäkinen and Isomäki, 2004). Larger trees by definition have a greater height and diameter resulting in a larger cambium surface area than smaller trees. This larger surface area results in greater volume accumulation in dominant trees, even when radial growth is similar for the three social statuses.

In terms of relative growth, however, suppressed trees showed the greatest positive response to treatments, followed by co-dominant and dominant trees. The factors at play here are related to differences both in growing conditions and growth potential of trees between the different social classes. According to Vincent et al. (2009), dominant trees are generally least affected by thinning because their relatively large crowns situated in and above the upper canopy already benefit from the highest levels of direct light exposure of all trees in a stand. While they can maintain their good absolute growth rates, the relative effect of thinning on their growing environment is therefore less than for trees in the mid- to lower-canopy. Moreover, the capacity of dominant trees to respond to treatments, particularly if they are old and/or approaching maximum height, may be limited.

In contrast, the potential change in the light environment of suppressed (and to a lesser extent, co-dominant) trees induced by partial harvesting treatments is much greater. As well, while early suppression limits height growth of suppressed trees and postpones the time at which maximum growth rate is reached, it does not necessarily inhibit their growing capacity (Assmann, 1970), so the greater change in the light environment and the growth potential of suppressed trees both contribute to explaining their superior relative growth.

Although all trees responded positively to partial harvesting, growth responses were proportional to their pre-treatment growth rate: less vigorous trees with slower pre-treatment growth rates continued to exhibit slow but improved post-treatment growth rates while more vigorous, younger trees continued to have highest growth rates post-treatment. The effect of

pre-treatment tree vigour on post-treatment growth has also been found for black spruce (Thorpe et al., 2007) and trembling aspen (Bose et al., 2014) in eastern Canada.

2.6.4 Neighbourhood competition

Neighbourhood competition indices are generally based on the size ratio of target and neighbour trees and assume that competition decreases with increasing distance to neighbour tree but increases with increasing neighbour size. We used a series of simple indices based on Hegyi's competition index (1974) because it is easily computed yet has proved to be effective (Avery and Burkhart, 2002; Filipescu and Comeau, 2007; Neufeld et al., 2014).

Across all treatments, average radial and volume growth in years 8, 9 and 10 post-treatment was negatively influenced by neighbourhood competition. Aspen is generally considered to have the competitive advantage in mixed stands on productive sites, such as the ones in this study (Wagner, 2000; Boivin et al., 2010), primarily due to its superior juvenile growth rate which allows trees to attain canopy dominance and capture more resources, particularly light (Balandier et al., 2006). It was therefore expected that aspen would exhibit a strong competitive effect on the white spruce. Indeed, it was a fundamental assumption in the design of the harvesting experiment.

Somewhat surprisingly, results indicated that coniferous competition had a greater effect on white spruce growth than deciduous competition. This concurs with Stadt et al. (2007) and Huang et al. (2013) who, through the use of more complex competition indices, also found that intraspecific competition caused greater reductions in white spruce growth than aspen competition. In Quebec mixedwood stands similar to but younger than those in this study, Boivin et al. (2010) found that conspecific neighbours were stronger competitors affecting balsam fir growth, and that aspen was the weakest competitor among the four species evaluated in their study. They suggest that high densities of aspen in mixedwood stands are more related to the species' ability to vegetatively reproduce through root suckers and grow quickly, rather than a particularly strong capacity to compete.

The results of this study are further supported by the work of Fradette (2014), who found that competition in 15 to 30 year old white spruce plantations was primarily intraspecific but also strongly affected by other conifer species like balsam fir. High levels of competition for light from spruce (and fir) is attributed to the large crowns and persistent foliage of these conifers. As well, close proximity of conspecific neighbours can cause negative physical interactions between the crowns and inhibit crown expansion and radial growth (Canham et al., 1994; Power et al., 2012). Fradette (2014) also found that aspen was a weak competitor for white spruce and that competition was only likely to be significant if aspen density was high and produced a high shading effect. Higher light transmission levels in aspen canopies are related to morphological and physiological differences between the two species, notably aspen's lower leaf biomass, particularly during the spring and fall when aspen have lost their leaves (Lieffers and Stadt, 1994; Constabel and Lieffers, 1996; Man and Lieffers, 1999). This supports the present findings that aspen was not a strong competitor and would explain why positive growth responses in white spruce occurred only after 100% removal of aspen.

Radial growth was negatively influenced by conifer trees located anywhere within a 5 m radius to the white spruce trees regardless of actual proximity. Alternatively, volume growth was negatively affected by conifer trees within a 10 m radius, with both DBH and proximity of neighbour trees influencing the competitive effect. Diameter growth has long been known to be more sensitive to competition (stand density) than height growth (McClain et al., 1994; Jobidon, 2000; Wagner, 2000; von Oheimb et al., 2011). Once respiration demands have been met, carbon allocation is prioritized to height growth before diameter, and as a result height growth is less affected by neighbour density and thinning prescriptions (Wagner, 2000). This suggests that conifer specific neighbourhood competition within the immediate vicinity of the white spruce trees are regulating their diameter growth, but not necessarily height and volume growth (von Oheimb et al., 2011).

2.6.5 Management implications

As forest companies in eastern Canada increasingly intervene in aspen-dominated mixed stands, new opportunities will emerge to refine harvesting practices in order to take advantage of differences in competitive and treatment effects, tree size and growth potential

of the component species. In the mixed aspen-white spruce stands studied here and elsewhere (Stadt et al., 2007; Huang et al., 2013), spruce growth is primarily affected by competition from conifers (spruce and balsam fir) and only showed a significant growth response to 100% removal of aspen stems. While large white spruce stems accrue more volume than smaller stems, the relative response of suppressed stems to partial harvesting is considerably greater than stems in co-dominant and dominant classes. Younger, vigorous stems have greatest relative growth increases and the greatest potential for sustained positive growth increment following partial harvesting. Therefore, with an adapted prescription, a regular shelterwood or heavy commercial thinning treatment with a final cut in 10 to 20 years could result in significant tree volume increments between initial and final harvests. In mixedwood stands with an important spruce component in all canopy layers, a heavy partial cut or complete removal of aspen stems, accompanied by harvesting a portion of the largest and presumably oldest spruce, and thinning of other crowded spruce, should result in positive growth response of both residual spruce in the lower to mid canopy and residual aspen stems in the upper canopy (Bose et al., 2014). This recommendation is based on potential effects on growth of residual stems only; regeneration dynamics were not part of the present study and certainly must be considered in the evaluation of such a harvesting option. Finally, because partial harvesting treatments result in rapid growth and often delay crown recession, residual trees are prone to increased stem taper. A detailed evaluation of growth allocation along the length of the stem accompanied by an assessment of wood quality properties of residual trees, would provide a better indication of the success of these harvesting prescriptions.

2.7 Conclusion

Boreal mixedwood stands vary in their composition and structure but some common patterns, notably the transition from intolerant hardwood dominance to conifer or mixed-conifer dominance, characterize their successional dynamics. Integrated mixedwood management increasingly promotes the maintenance of a broad range of mixedwood stand types across forest landscapes, and the efficient exploitation of both the hardwood and softwood components in mixed stands. The results presented here demonstrate that white spruce trees are capable of accelerated growth following aspen canopy removal, but only when aspen

harvesting is severe (100%) and total stand basal area removal is high (64-83%). In contrast with previous studies, growth response was detectable within the first two years following treatment and growth rates largely depended on tree social status and vigor prior to treatment. Longer term monitoring is required to evaluate regeneration dynamics since heavy recruitment of aspen could influence white spruce regeneration and growth in the future. Tree mortality was not evaluated in this study, but would provide another indication of how trees acclimatize to severe canopy opening. In the context of increased ecosystem-based forest interventions in mixedwood forests, the results of this study should contribute to the refinement of partial harvesting treatments that integrate natural stand dynamics and concerns for maintaining forest productivity.

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CHAPTER III

GENERAL CONCLUSION

3.0 Conclusion

As harvesting has intensified throughout Quebec's boreal forest, and the cumulative effects of even-aged management on forest composition and age structure have come to light, there has been growing interest in developing sound silvicultural alternatives to CPRS and variants of clear-cutting. In the context of forest ecosystem management (FEM), silvicultural treatments that emulate natural disturbances and successional dynamics have been recommended as a means of increasing stand- and forest-level structural diversity and mitigating some of the negative impacts of strict even-aged management regimes. In this respect, partial harvesting has been proposed as a viable complement to conventional management with the potential to balance the goals of ecosystem management with economic objectives, such as maintained or increased wood production (Harvey et al., 2002; Comeau et al., 2005). According to Bergeron et al. (2009), although such treatments do not perfectly emulate natural dynamics, they should be designed and implemented in a manner that maintains natural ecosystem processes and attributes and at scale that corresponds to the frequency and severity of natural disturbances.

In aspen-dominated boreal mixedwood stands where white spruce reaches its maximum annual growth increment later than aspen, partial harvesting could increase stand productivity if each species is harvested at its optimum moment of development, generally aspen first and spruce later. It is in this context that experiments developed to test and evaluate silvicultural treatments consisting of canopy aspen extraction and the retention of pre-commercial and small merchantable white spruce (and other tolerant conifer) trees find their relevance. An added benefit to partial harvesting is that residual trees typically exhibit accelerated growth rates as they are released from competition. Despite the potential benefits of partial harvesting, few studies have actually evaluated the growth responses of residual trees in boreal mixedwood stands, particularly in eastern Canada. Even fewer have used stem analysis to study longer-term volume growth responses of white spruce trees subjected to partial harvesting treatments in which canopy aspen is removed.

The abundance of good quality white spruce trees, many of which were premature, in the stands of the present study provided the primary incentive for initiating this partial harvesting

experiment. Initial objectives were to encourage white spruce regeneration and stimulate growth responses in residual white spruce stems through aspen removal; the present study concentrated on the latter objective. This type of treatment is not common in eastern Canadian boreal mixedwoods because of the many constraints associated with partial harvesting, including higher costs associated with multiple interventions, lower initial economic returns and longer time horizons involved (Bose et al., 2013).

3.1 Summary of results

The primary objective of this project was to evaluate the effect of partial harvesting on the growth of residual white spruce trees over a period of ten years post-treatment. We investigated the effect of treatment intensity by measuring white spruce growth across a gradient of partial harvesting intensities involving four proportions of aspen basal area (BA) removal (0, 50, 65 and 100%). A severe cutting intensity of 100% aspen removal was necessary to induce accelerated radial and volume growth rates in canopy (suppressed to dominant) white spruce trees. Growth response was apparent within the first two years following treatment, indicating that the trees did not suffer from growth stagnation following harvesting. While radial growth peaked at approximately six years post-treatment, volume growth continued to increase throughout the ten years following treatment.

We also determined that tree social status was an important predictor of the magnitude of growth response. In terms of absolute volume growth, dominant trees exhibited superior growth rates than co-dominant and suppressed trees. This was likely due to their greater initial height and circumference, which provided them with a greater capacity to accumulate wood. In relative terms, however, suppressed trees showed the greatest improvement in cumulative growth, probably because they had higher growth potential than co-dominant and dominant trees and because they experienced the greatest change in environmental conditions following harvesting. All three social statuses responded similarly in terms of radial growth, but more vigorous trees with higher pre-treatment growth rates continued to have superior growth rates post-treatment.

Furthermore, we used Hegyi's competition index to assess the influence of neighbouring trees on the growth rates of each sampled spruce in the last three years (8-10 years) following treatment. While aspen is often perceived to be a strong competitor of white spruce, our results indicated that coniferous competition had a greater effect on white spruce growth than deciduous competition. Radial growth was regulated by conifer neighbours situated anywhere within 5 m of the sampled white spruce trees. In contrast, volume growth was negatively affected by conifer trees within a 10 m radius, with both DBH and proximity of neighbour trees influencing the competitive effect.

3.2 Future considerations

For the studied stands, future harvesting depends on longer term objectives and whether they are strictly related to timber production or include other purposes, such as those related to maintaining structural and habitat diversity, as well as other ecosystem values. Depending on the amount and configuration of trees left following partial harvesting, residual forest cover will tend to maintain some attributes and functions of the original, intact stand (Ruel et al., 2013). In many forests these "biological legacies" have been shown to be important for the maintenance of biodiversity and biogeochemical cycling (Vanderwel et al., 2009; Gustafsson et al., 2012) and this residual forest cover likely maintains a more complex structure than what would be found following a CPRS or clear-cut.

At the time of partial harvesting, a second and likely final cut was tentatively planned for approximately fifteen years post-treatment. Although the composition and structure of these stands potentially lend themselves well to subsequent "alternative treatments", under current standard practices, the most likely treatment would consist of a CPRS harvest, whether white spruce regeneration has established in the interim or not. If this comes to fruition, it would be difficult to judge whether such partial harvesting treatments with high canopy aspen removal are justifiable. Although white spruce showed accelerated radial and volume growth at the tree level, the removal of the aspen trees ultimately reduced total stand volume and BA which could not be recovered to pre-treatment levels over such a short time frame. That being said, individual tree value and stand value may be improved since larger, more valuable and easier to process stems can be produced.

Although our results demonstrate that white spruce trees exhibit positive growth responses following removal of canopy aspen, residual tree growth represents only one measure of the success of partial harvesting. In order to evaluate the full potential of the silvicultural treatments employed in this study, future work should concentrate on assessing tree regeneration and mortality. White spruce and aspen regeneration in the four treatments should be evaluated since this will have a direct influence on the composition of the future stands. If treatment objectives include hastening the transition of these stands to conifer dominance and they are to be retained on a longer term, white spruce regeneration would need to be high and aspen suckering relatively low. Since white spruce trees in these stands were primarily in the large sapling and merchantable size classes, and therefore well-established at the time of treatment, regenerating aspen in the 100% treatment was unlikely to have restricted growth of white spruce sapling and tree stems during the 10 year post-treatment period. However, aspen regeneration by suckering can be prolific and fast-growing (Prévost and Pothier, 2003; Brais et al., 2004) and may pose a problem in the future if it over-tops and represses advanced regeneration and post-harvest recruitment of spruce seedlings. If this is indeed the case and residual white spruce stems are expected to survive and accrue volume, it is possible that the future harvest could be prolonged until the regenerating aspen has reached maturity, at which time both the residual white spruce and aspen could be harvested. Furthermore, tree mortality, which we did not quantify for the 10 year period following harvesting, can be high when residual stand BA is low (Thorpe and Thomas, 2007). Mortality can occur as a direct result of damage during harvesting operations or because trees fail to acclimatize to the environmental changes induced through severe canopy opening (Thorpe and Thomas, 2007). Mortality in the treated stands should be evaluated since tree loss (and product recovery) ultimately affects the profitability of partial harvesting and subsequent treatments.

The fact that conifer trees had a strong competitive effect on radial and volume growth of white spruce suggests that removing some dominant white spruce trees and over-crowded conifer stems at the time of aspen removal could result in even greater treatment growth responses. Conifer-specific competition probably kept suppressed and co-dominant tree growth in check in the partially cut stands. Trees in these social classes have the greatest

potential for increases in commercial value because they exhibit the greatest magnitude of relative growth response. Moreover, if social status reflects tree age, their positive growth response should be sustained longer than that of older dominant stems.

Crown characteristics and stem taper are influenced by the crowding of neighbouring trees. Thinning treatments that reduce crowding often produce trees with comparatively longer crowns than those of unthinned trees and these longer crowns continue to allocate growth in lower parts of the stem (Karlsson, 2000; Mäkinen and Isomäki, 2004; Power et al., 2012). High stem taper tends to reduce stem value and often complicates wood processing (Tong and Zhang, 2008). If stem taper is high, the benefits of increased volume accumulation (product recovery) resulting from partial harvesting (and thinning) could be negligible if it does not increase the value of the stems that are to be used for saw logs. In such a case, partial harvesting treatments (even those with additive yields of hardwoods and softwoods) may not be considered economically acceptable. Therefore, the commercial viability of these types of partial harvesting treatments should also be assessed to determine whether the increased tree growth offsets the costs of initial harvest and future interventions.

3.3 Research contribution

This thesis encompasses one sub-project of a much more comprehensive research initiative currently undertaken at the University of Quebec in Abitibi-Témiscamingue (UQAT) in collaboration with the Centre for Forest Research, the UQAT-UQÀM Industrial Chair in Sustainable Forest Management (Chaire AFD), the Canadian Forest Service and the industrial partners Tembec Industries and Norbord Industries. This larger project was initiated to address a broad range of research questions that will help advance our knowledge and understanding of boreal mixedwood dynamics in eastern Canada and aid in the development of sound silvicultural approaches better suited to mixedwood stand types.

In general, the results of this project contribute to a growing body of knowledge concerning the efficacy and suitability of applying partial harvesting in the boreal forest. More specifically, this study provides quantitative information regarding the magnitude of white spruce growth responses to a variety of partial harvesting intensities, the duration of response

and the factors affecting tree growth, including tree social status, pre-treatment growth rate and neighbourhood competition. This information should aid in validating the feasibility of partial harvesting and in the refinement and adaption of treatments to specific boreal mixedwood stand conditions. The boreal forest is deeply ingrained in Canada's national identity and, as such, we must work towards balancing the ecological, social and economic services it provides.

ANNEX A

SUPPLEMENTARY FIGURES

Experimental units were laid out based on prism inventories completed prior to partial harvesting. Harvesting treatments consisted of a no-harvest control, (0% BA removal), two intermediate treatments that removed 50 and 65% of aspen BA and an extreme treatment of 100% aspen BA removal. Each treatment was repeated three times for a total of twelve experimental units.

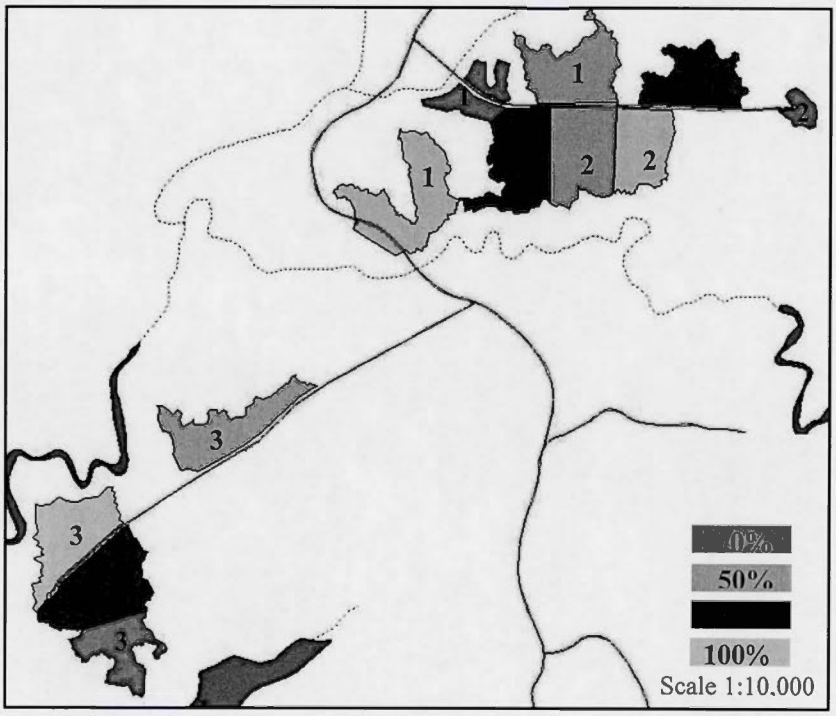

Figure A.1 Spatial arrangement of experimental units and treatment replications.

Cross sectional disks were sampled from 11 positions along the length of the stem of each sampled white spruce tree. The first two disks were sampled from fixed heights of 0.3 and 1.3 m, while the remaining nine disks were sectioned from equally spaced positions along the length of the stem from 1.3 m to the top of the tree. Fig. A. 2 provides a visual representation of the spruce stem and sampling heights.

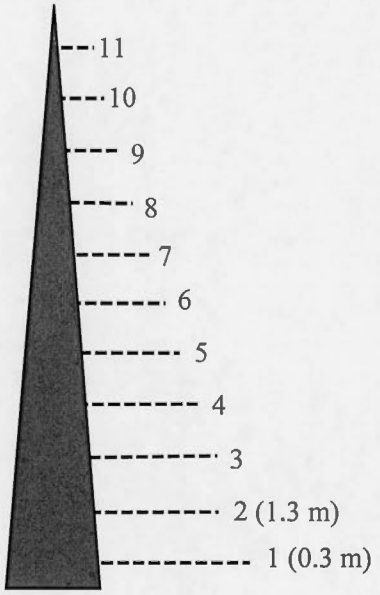

Figure A.2 Relative position of cross sectional disks sampled from 72 white spruce trees (adapted from Chhin et al., 2010).

Minimum age of sampled white spruce was based on cambial age from disks taken at 0.3 m while minimum aspen age was determined by coring (at 1 m) the nearest aspen tree (≥ 20 cm DBH) to each sampled white spruce. Mean white spruce and aspen ages were 71 and 68, respectively. While some old (100 to 120 years) white spruce trees were present in stands, roughly 89% of sampled trees established within 14 years, corresponding to calendar years 1937 to 1950. Aspen establishment generally occurred throughout the same time period, but recruitment was more gradual.

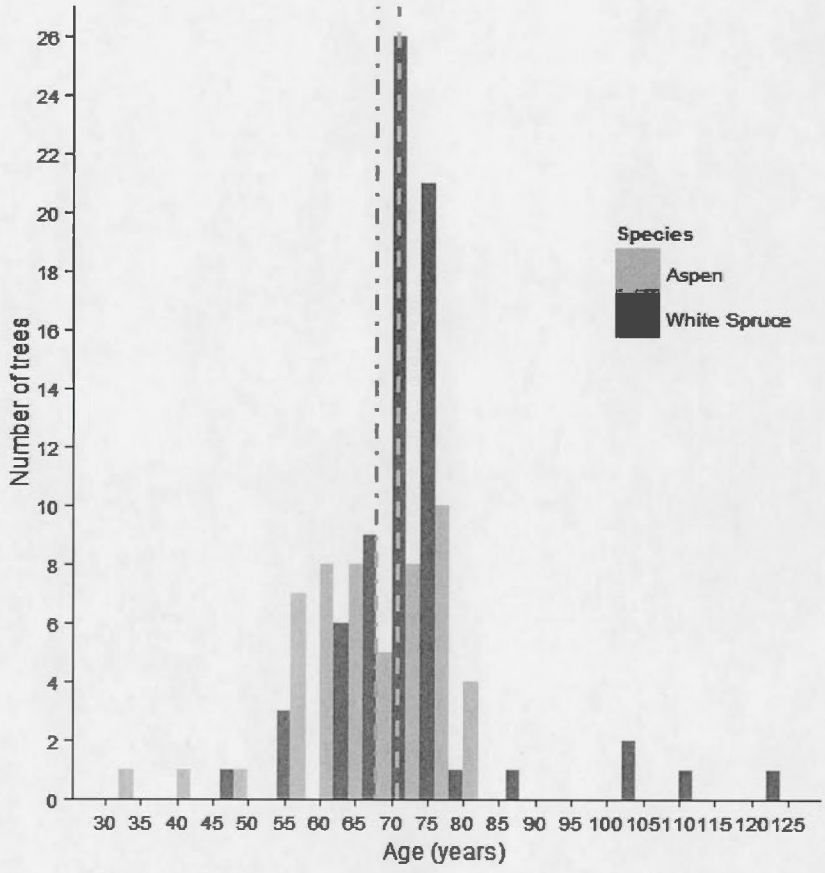

Figure A.3 Age distribution of sampled white spruce and aspen trees. Mean age of white spruce was 71 (teal dashed line) while mean age of aspen was 68 (orange dot-dash line).

We used tree diameter distribution as a proxy for height distribution and social status in each experimental unit. Also, given that aspen generally occupied the dominant canopy social class with only a minor component of spruce, assignment of social status to individual spruce stems was based exclusively on the relative size among the white spruce trees (relative intraspecific canopy position), rather than the true interspecific social status of all trees within the stand. Stem size distribution was calculated for each experimental unit based on white spruce trees in the permanent sample plots (PSPs) and the following classification was used to select individual trees to be destructively sampled from each social status class: dominant trees: diameter size class ≥ 2 standard deviations (SD) of mean DBH; co-dominant trees: size class of ≥ 1 SD of mean DBH; suppressed trees ≤ the mean DBH.

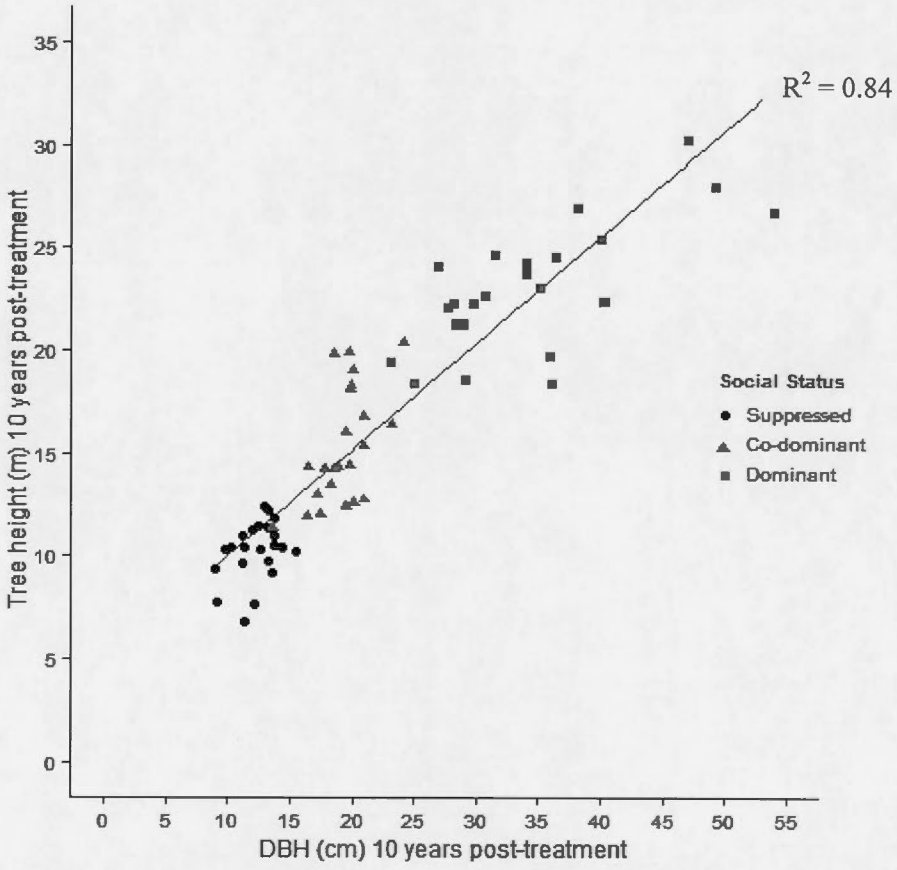

Figure A.4 Relationship between diameter at breast height (DBH) and tree height of sampled white spruce trees in 2012.

Social status at the time of treatment was maintained throughout the post-treatment period; that is, an individual's social status did not change as a result of treatment.

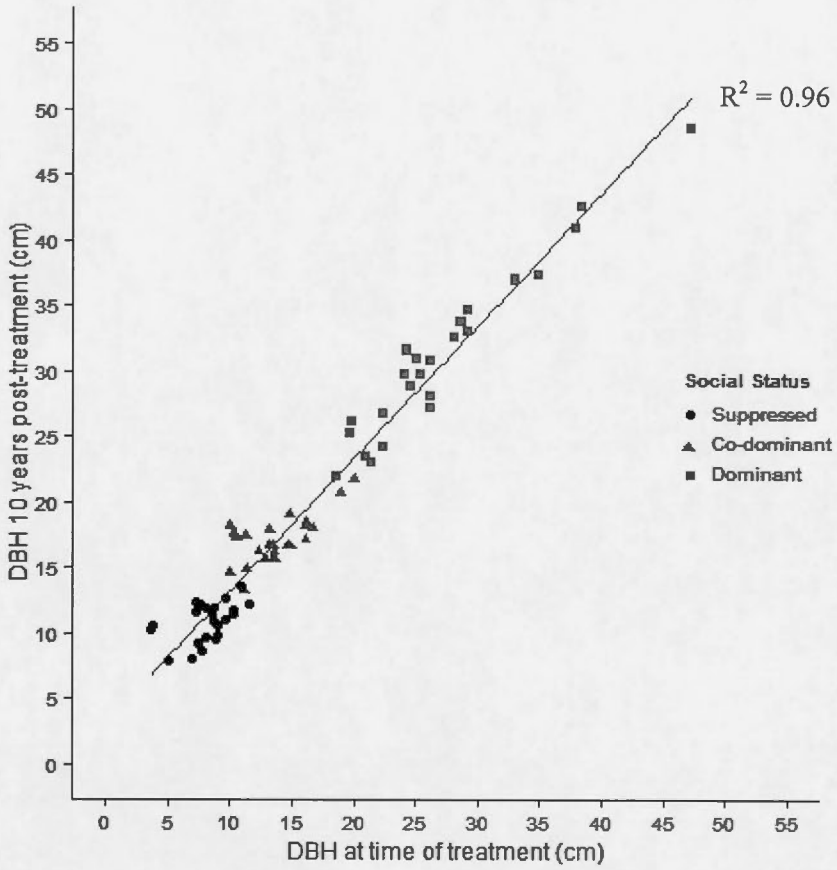

Figure A.5 Diameter at breast height (DBH) of sampled white spruce trees at the time of partial harvesting and ten years post-treatment.

Crown length of the sampled white spruce trees was measured at the time of sampling in 2012. As expected, crown dimensions were strongly influenced by tree social status with dominant trees having longer crowns than co-dominant and suppressed trees.

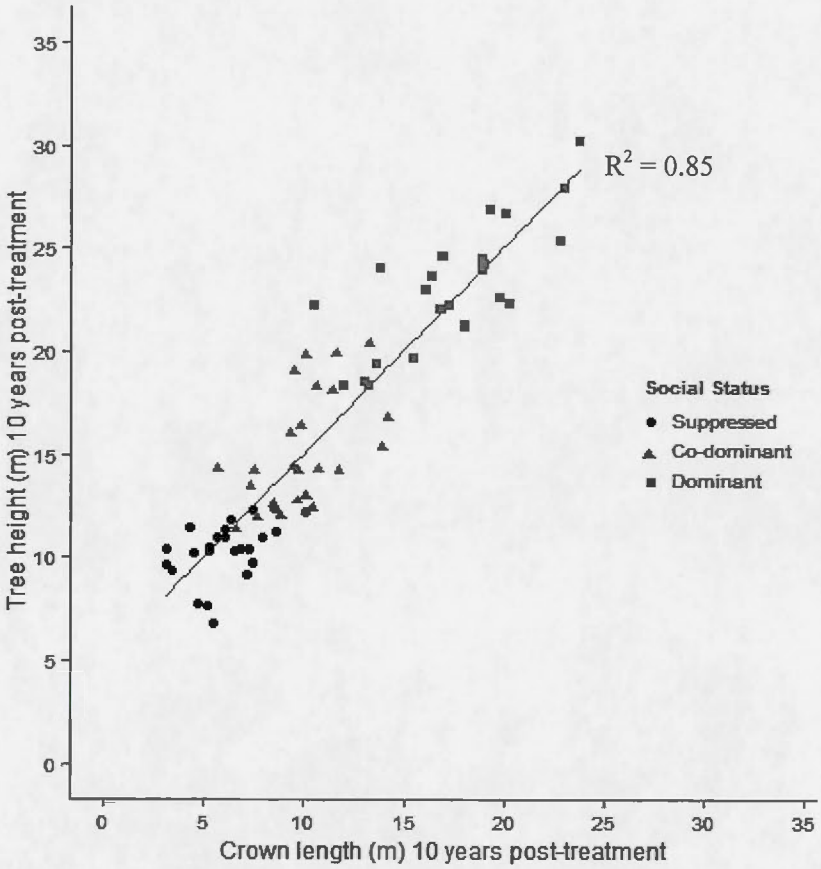

Figure A.6 Relationship between crown length and total tree height of sampled white spruce trees in 2012.

Cambial age at the time of treatment has a direct influence on increment growth potential. Young cambium is more effective in producing new wood cells and thicker annual rings than older cambium (Vaganov et al., 2006). Radial (and diameter) growth rates decrease after maximum annual increment has been reached so old trees tend have slower radial growth rates than younger trees of the same size (Jogiste, 2000).

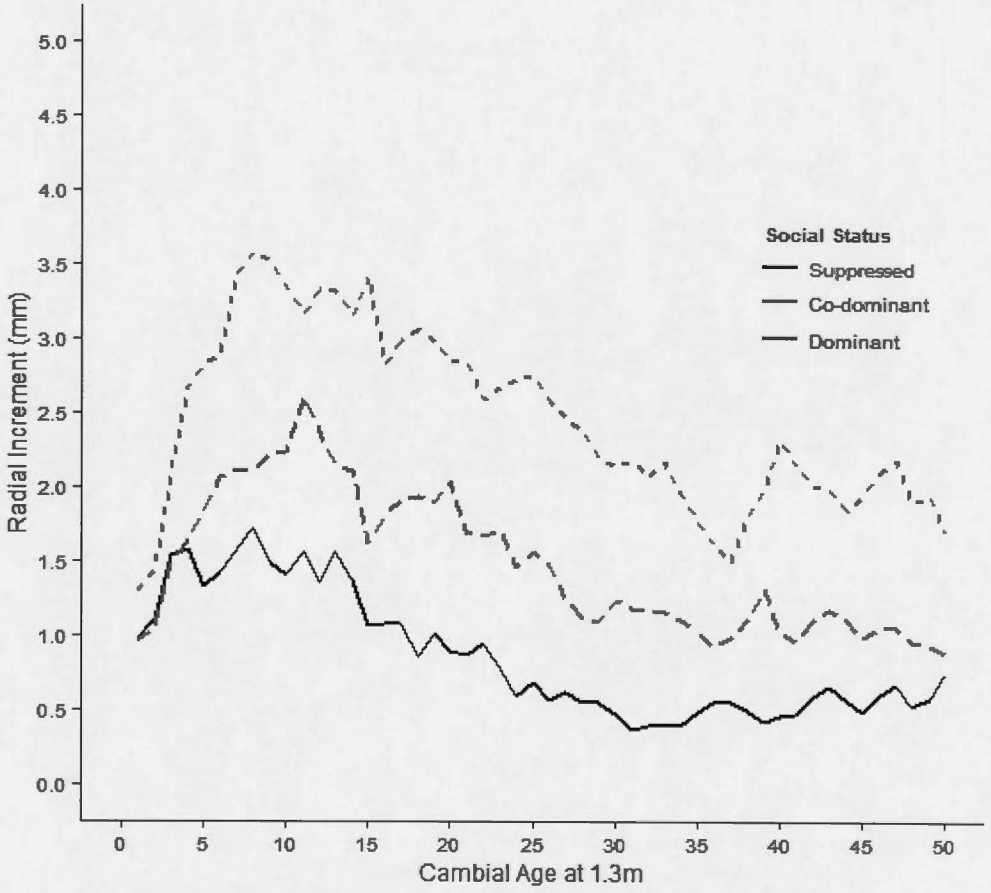

Figure A.7 Mean radial increment curves for dominant, co-dominant and suppressed white spruce trees sampled from control stands.

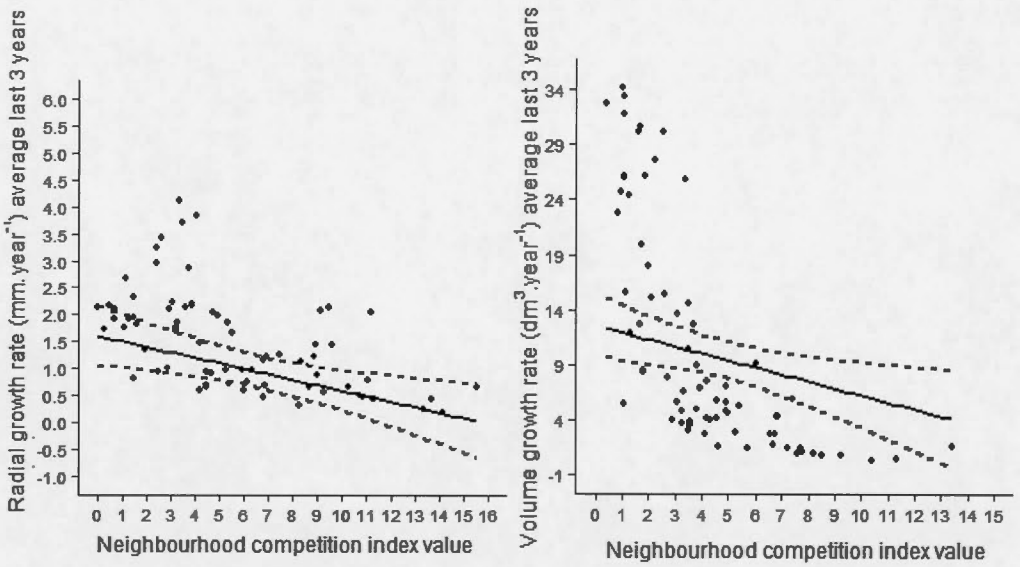

Figure A.8 Relationship between radial and volume growth rates and neighbourhood competition index values. Solid lines represent predicted values, dashed lines are 95% confidence intervals. Points represent observed values. Growth decreases with increasing neighbour competition.

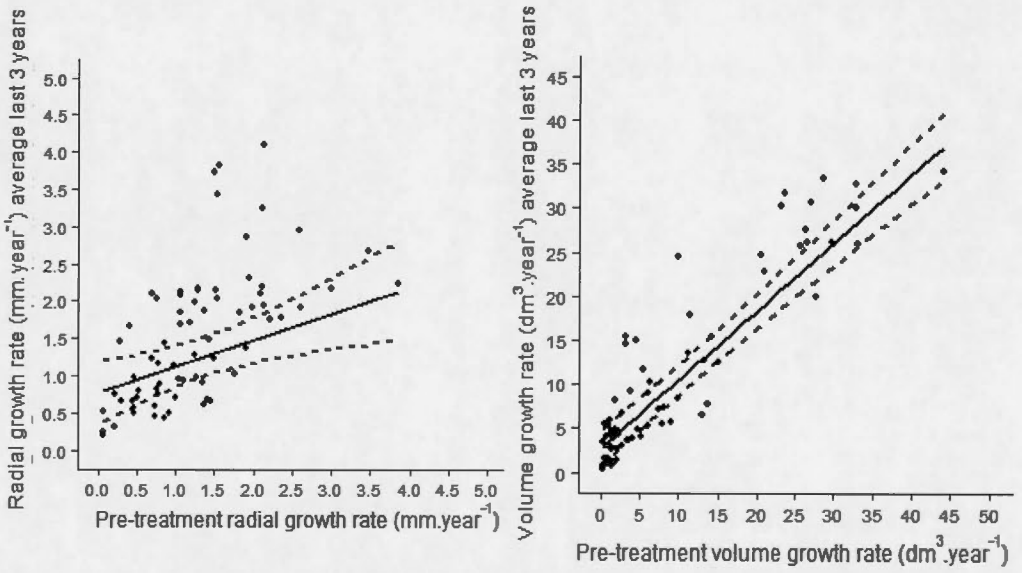

Figure A.9 Relationship between radial and volume growth rates and pre-treatment growth rate (average 5 years pre-treatment). Solid lines represent predicted values, dashed lines are 95% confidence intervals. Points represent observed values. Less vigorous trees with slower pre-treatment growth rates continued to exhibit slow but improved post-treatment growth rates while more vigorous, trees continued to have highest growth rates post-treatment.

ANNEX B

SUPPLEMENTARY TABLES

Table B.1 The 30 variations of Hegyi's neighbourhood competition index (HCI)

Model	Neighbour Tree Type	Distance Dependent	Distance to target white spruce tree
HCI1	All trees	No	0-10m
HCI 2	All trees	No	0-8m
HCI3	All trees	No	0-6m
HCI 4	All trees	No	0-5m
HCI 5	All trees	No	5-10m
HCI 6	Broadleaf	No	0-10m
HCI 7	Coniferous	No	0-10m
HCI 8	Broadleaf	No	0-8m
HCI 9	Coniferous	No	0-8m
HCI 10	Broadleaf	No	0-6m
HCI 11	Coniferous	No	0-6m
HCI 12	Broadleaf	No	0-5m
HCI 13	Coniferous	No	0-5m
HCI 14	Broadleaf	No	5-10m
HCI 15	Coniferous	No	5-10m
HCI 16	All trees	Yes	0-10m
HCI 17	All trees	Yes	0-8m
HCI 18	All trees	Yes	0-6m
HCI 19	All trees	Yes	0-5m
HCI 20	All trees	Yes	5-10m
HCI 21	Broadleaf	Yes	0-10m
HCI 22	Coniferous	Yes	0-10m
HCI 23	Broadleaf	Yes	0-8m
HCI 24	Coniferous	Yes	0-8m
HCI 25	Broadleaf	Yes	0-6m
HCI 26	Coniferous	Yes	0-6m
HCI 27	Broadleaf	Yes	0-5m
HCI 28	Coniferous	Yes	0-5m
HCI 29	Broadleaf	Yes	5-10m
HCI 30	Coniferous	Yes	5-10m

Table B.2 Fifteen competing models used to test the effects of treatment intensity (intensity), social status (ss), time, pre-treatment growth rate (pre-treat) and cambial age (age) on radial and volume growth rates of white spruce trees. Models 2 to 9 test the quadratic effect of time, models 10 to15 test the linear effect of time. Interactions between variables are specified with a colon.

Model	Biological interpretation
1. null	No effect of treatment, social status, time or pre-treatment growth on post-treatment growth.
2. age + time + time^2 + pre-treat	No effect of treatment or social status on post-treatment growth.
3. age + intensity + time + time^2 + pre-treat	The effect of treatment is the same across time, no effect of social status.
4. age + intensity + ss + time + time^2 + pre-treat	The effect of treatment is the same across time and assumes no differences in growth between social statuses across all treatments.
5. age + ss + time + time^2 + pre-treat	There are no differences in growth between social statuses across all treatments and time.
6. age + intensity + ss + time + time^2 + pre-treat+ intensity:time + intensity:time^2	The effect of treatment differs across time and assumes no differences in growth between social statuses across all treatments.
7. age + intensity + ss +time + time^2 + pre-treat + intensity:ss	The effect of treatment is the same across time but growth differs for trees of different social statuses depending on treatment intensity.
8. age + intensity + ss + time + time^2 + pre-treat + ss:time + ss:time^2	The effect of treatment is the same across time but growth differs for trees of different social statuses across time.
9. age + time + pre-treat	No effect of treatment or social status on post-treatment growth.
10. age + intensity + time + pre-treat	The effect of treatment is the same across time periods, no effect of social status.
11. age + intensity + ss + time + pre-treat	The effect of treatment is the same across time and assumes no differences in growth between social statuses across all treatments.

12. age + ss + time + pre-treat	There are no differences in growth between social statuses across all treatments and time.
13. age + intensity + ss + time + pre-treat + intensity:time	The effect of treatment differs across time and assumes no differences in growth between social statuses across all treatments.
14. age + intensity + ss +time + pre-treat + intensity:ss	The effect of treatment is the same across time but growth rates differ for trees of different social statuses depending on treatment intensity.
15. age + intensity + ss + time + pre-treat + ss:time	The effect of treatment is the same across time but growth differs for trees of different social statuses across time.

Table B.3 Nine competing models used to test the effects of treatment intensity (intensity), social status (ss), pre-treatment growth rate (pre-treat), neighbourhood competition index (HCI) and cambial age (age) on radial and volume growth rates of white spruce trees. Interactions between variables are specified with a colon.

Model	Biological interpretation
1. null	No effect of treatment, social status, pre-treatment growth rate or competition on average annual growth in last 3 years.
2. age + intensity + pre-treat	Growth differs depending on treatment but assumes no differences in growth between social statuses.
3. age + ss + pre-treat	Growth differs depending on tree social status but assumes no differences in growth between treatments.
4. age + HCI + pre-treat	Growth differs depending on neighbourhood competition but assumes no differences in growth between social statuses or treatments.
5. age + intensity + HCI + pre-treat	Growth differs depending on treatment and neighbourhood competition but assumes no differences in growth between social statuses.
6. age + intensity + ss + pre-treat	Growth differs depending on treatment and tree social status but assumes no differences in neighbourhood competition amongst the treatments.
7. age + intensity+ HCI + pre-treat + HCI:intensity	Growth differs depending on neighbourhood competition but assumes no differences in growth between social statuses. The effect of competition differs depending on the treatment.
8. age + intensity + ss + pre-treat + ss:intensity	Growth differs depending on social status but no difference in neighbourhood competition amongst the treatments. Growth of trees within a social status differ depending on treatment intensity.
9. age + pre-treat	Growth depends on pre-treatment growth and assumes no effect of treatment, social status or neighbourhood competition.

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GENERAL INTRODUCTION AND CONCLUSION

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